Analysis of the “nurse-tree effect“ of exotic shelter trees on the growth of the indigenous *Podocarpus falcatus* in an Ethiopian montane forest

Dissertation

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1 Introduction

1.1 Forests in Ethiopia

In Ethiopia, like in most tropical countries, deforestation is one of the major environmental hazards. Many forests have been reduced to a small fraction of their original size and their destruction continues at a rapid rate. The natural high forests of Ethiopia which were estimated to have once covered 40% of the country (von Breitenbach 1962), declined to only 13.7% in the 1990's and to 11.5% in 2010 (FAO 2010). Today, Ethiopian forests disappear at a rate of 1.1% (140,000 hectares) per year (FAO 2010). In some parts of the country the decline of forests was even more severe resulting in a forest cover of 0.3 to 4% already in 2000 (Zeleke and Hurni 2001; Dessie and Kleman 2007; Garedew et al. 2009). While central and northern Ethiopia is largely deforested, remaining areas of tropical high forests are still found in the less populated southern and western parts of the country. Mixed evergreen forests with *Podocarpus falcatus, Croton macrostachyus, Olea capensis, Prunus africana, Syzygium guineense,* and *Hagenia abyssinica* occur at higher altitudes in southern Ethiopia and in the central highlands (Fetene and Feleke 2001; Tesfaye et al. 2002).

Due to the lack of alternatives for energy supply, 90% of the annually produced wood is used for fuel (Teshome 2009). To protect the remaining parts of the natural forest and to meet the requirements of the people, fast growing exotic tree plantations were established in the 1950's (Pohjonen and Pukkala 1990). Trees like pine (*Pinus patula*), eucalypt (*Eucalyptus saligna*, *globulus* and others) and cypress (*Cupressus lusitanica*) were planted on large scale for reforestation in areas where farmland has replaced the natural forest already in earlier times. In spite of serious appeals illegal cutting of indigenous forests for farmland or more profitable exotic tree plantations continues still today.

1.2 The Munessa-Shashamene Forest

One of the large Ethiopian forests is the Munessa-Shashamene Forest, an afromontane forest on the eastern escarpment of the Rift Valley. Centuries ago, this forest area was inhabited by nomadic people, but in the nineteenth century land use changed from nomadic to sedentary (Assefa 1996). Large scale forest utilisation started in the 1940's when the first sawmills were established (von Breitenbach 1961). Subsistence farmers

and saw-millers used the forest to a great extend, resulting in a change of the forest into pasture and arable land. Plantations with exotic tree species began in the late 1950's and early 1960's (Lundgren 1969), and at larger scale in the seventies (Hvidberg-Hansen 1977). Most of the plantations in the Munessa-Shashamene Forest were established on disturbed forest areas, remnants of the natural forest were cleared and burnt prior to the establishment of the plantations. In the 1990's, the Munessa-Shashamene Forest came under the administration of the Munessa-Shashamene Integrated State Forestry Development and Utilization Project (the so-called Forest Enterprise) which is still managing the plantations. The forest has a total area of 23,000 ha, of which about 30% have been converted to plantations of the exotic tree species *Cupressus lusitanica* (62.7%), *Eucalyptus spp.* (27.1%), *Pinus patula* (5.6%) and others (4.6%) (Senbeta et al. 1999; Ayane 2008).

The plantations in the Munessa-Shashamene Forest and the remaining patches of natural forest border each other. The natural forest in the Munessa-Shashamene Forest represents the typical vegetation between 1800 and 2800 m a.s.l. dominated by *Podocarpus falcatus* (Podocarpaceae*)* which grows up to 50 m high (Russ 1945) (Figure 1). The forest consists of a mixture of evergreen and a few deciduous woody species (Chaffey 1980; Mueller-Hohenstein and Abate 2004). Other main canopy species are *Syzygium guineense* (Myrtaceae), *Pouteria adolfi-friederici*, *Prunus africana* (Rosaceae), *Croton macrostachyus* (Euphorbiaceae), *Juniperus procera* (Cupressaceae) and *Olea capensis* (Oleaceae) (Chaffey 1980; Mueller-Hohenstein and Abate 2004). The understory consists mainly of smaller trees and larger shrubs like *Bersama abyssinica*, *Brucea antidysenteria*, *Calpurnina aurea*, and *Discopodium penninervium* (Abate 2004). The highly disturbed natural forest is shrinking quickly and is in danger of loosing its biological diversity due to uncontrolled and illegal logging, collection of firewood and the tendency of the local people to expand their farm land. Due to ongoing disturbance of the forest, regeneration of the indigenous tree species has become a major problem (Teketay 1997b; Tesfaye et al. 2010).

Figure 1: Mature Podocarpus falcatus at the edge of the natural forest, with the typical stem growth with peripheral strands occurring in older trees. For an estimation of the size compare the person at the base of the stem.

1.3 Impact of exotic tree plantation on the environment and the rejuvenation of indigenous trees

There is an ongoing discussion about the benefits and disadvantages of creating plantations of exotic tree species in the tropics. The advantage of such plantations is manifold: The trees are easy to cultivate from seeds in nurseries or by natural seeding in the forests, they are fast growing and produce a high amount of biomass in a relatively short time period and due to the straight growth of the pole they are sought for timber and construction wood while the branches and other remainders can be used as firewood. Non-timber products are also popular, e.g. tall pieces of *Cupressus* bark, which are used for bee hives and for coffins. But there are also considerable direct and indirect environmental problems associated with exotic plantations: Long-living monocultures are always threatened by pest calamities such as aphids (Watson et al. 1999; Mamo and Sterba 2006), however, which have already destroyed large

plantations of *Cupressus lusitanica* in East Africa. *Eucalyptus* is planted everywhere in Ethiopia and such plantations are reported to damage the ecosystem due to the high demand of water and nutrients of the trees (Poore 1985) and because the leaves, bark and roots release allelopathic substances which inhibit the growth of a ground vegetation (Lisanework and Michelsen 1993; Michelsen 1993). Needles of coniferous species, such as pine, contain high concentrations of aromatic and acidic low molecular compounds which are released upon litter decomposition into the soil (Fernandez et al. 2006) and may thus acidify the upper soil horizons which harbour a high proportion of the fine roots. Furthermore litter decomposition and nutrient release is inhibited by an acid milieu, and cationic nutrients are leached from the soil into the ground water, especially in regions with high precipitation (Poore 1985; Florence 1986; Yirdaw 2001). Considering the environmental deterioration caused by monotonous plantations of the commonly used exotic trees the chance of indigenous woody plants to get a foothold and rejuvenate naturally in those plantations appears to be very small. However, such judgements require more detailed consideration.

1.4 The “nurse-tree effect”

Recent studies demonstrated a potential of exotic tree plantations to promote the regeneration of tropical indigenous tree species (Parrotta 1992; Parrotta 1995; Fimbel and Fimbel 1996; Harrington and Ewel 1997; Keenan et al. 1997; Oberhauser 1997; Ashton et al. 1998; Otsamo 1998; Lemenih 2006; Kasenene 2007; Selwyn and Ganesan 2009). Depending on the former vegetation, the climate, and the exotic tree species used for afforestation or reforestation, positive or negative effects on soil hydrology (Huber et al. 2008; Little et al. 2009), soil physical and chemical properties (Binkley and Resh 1999), litter und nutrient turnover (Brasell and Sinclair 1983; Lisanework and Michelsen 1993) and soil carbon stocks (Guo and Gifford 2002) prevail. Monocultures of fast growing exotic species change dynamics of soil processes usually more than plantations of slowly growing trees (Little et al. 2009). Regeneration of forests of indigenous trees under the shelter of exotic trees, e.g. various species of *Pinus* and *Eucalyptus,* has been studied in many regions, especially in Central America (Parrotta 1995; Haggar et al. 1997; Montagnini 2001; Healey and Gara 2003; Cusack and Montagnini 2004) and Ethiopia (Pohjonen and Pukkala 1990; Michelsen 1993; Senbeta et al. 2002; Lemenih et al. 2004; Yirdaw and Luukkanen 2004; Lemenih and Teketay 2005). Enhanced growth of young indigenous trees under the canopy of an exotic

plantation has been termed the “nurse-tree effect” (Hardwick et al. 1997; Otsamo 1998; Santiago-Garcia et al. 2008).

Except in the interior of very dense plantations of *Cupressus lusitanica*, natural regeneration of indigenous tree species, in particular of *Podocarpus falcatus*, has been observed to various extents in the plantations of the Munessa-Shashamene Forest. This phenomenon has been addressed in several papers on the ecophysiology of the respective indigenous and exotic tree species (Fetene and Feleke 2001; Feyera et al. 2002; Luettge et al. 2003; Fetene and Beck 2004; Fritzsche et al. 2006). Surprisingly, the *Pinus patula* and *Eucalyptus saligna* plantations harbour a denser though unevenly distributed population of *Podocarpus* saplings than the natural forest, if the areas are not too far from a seed producing *Podocarpus* tree (Tesfaye et al. 2010). Even more unexpected was the observation that the saplings apparently perform similar or even better in the plantations than under the natural canopy (Tadele 2004). *Podocarpus falcatus* is known as a year round seeding tree (Tesfaye et al. 2010) whose seedlings and saplings are neither browsed by cattle and wildlife nor severely attacked by insects. A survival rate of 90% of the *Podocarpus* seedlings was recorded beneath the canopy of shelter-trees, whereas in full light and without shelter only 55% survived. After recruitment of the seedlings, relative growth rates were highest under moderate light (Tesfaye 2008; Girma et al. 2010). However, when a big *Podocarpus* tree begins to overtop the canopy of the other shelter-trees the leaves of its crown must fully adapt to the intense tropical light intensities. Such adaptation could take place already on the saplings stage, because after clear-felling of the exotic shelter-trees the *Podocarpus* saplings immediately reacted with enhanced growth converting the plantation into a close-to-nature forest which is dominated by *Podocarpus* (Figure 2).

Figure 2: *Eucalyptus* plantation about one year after clear-felling. Centre of the background: Some *Eucalyptus* trees were excepted from the felling action. Background right: A *Podocarpus* "mother tree" providing the seeds. Middle and foreground: *Podocarpus* saplings after removal of the coppiced *Eucalyptus* trees.

1.5 Aim of the study

The reasons of the "nurse-tree effect" are unknown as are the extents of the effect under different shelters. In the research area of the Munessa-Shashamene forest soils (Ashagrie et al. 2005) and the climate conditions are similar. Therefore the idea came up that differences in the microclimate under the various canopies are responsible for the differences in growth of the indigenous saplings. Major ecophysiologically relevant components of such microclimate are humidity and light (Chazdon and Fetcher 1984). Both factors control carbon gain by affecting stomatal conductance and photosynthesis. Effects of the structure of the canopy on the intensities of diffuse radiation and the temporal patterns of sunflecks are obvious (Chazdon and Pearcy 1986a; Pearcy 1990; Chazdon and Pearcy 1991; Lemenih et al. 2004; Leakey et al. 2005).

Therefore the hypothesis is put forward that varying patterns of irradiance and different contributions of sunflecks to the total photosynthetic active radiation (PAR) reaching the understorey represent the main factors for the performance and growth of the *Podocarpus falcatus* saplings under the shelter of the natural forest and exotic tree

monocultures. Other factors can be temperature and humidity, which, however, may not differ very much between the various neighbouring forest types. The hypothesis is supplemented by the assumption that competition for soil water between the saplings and the shelter-trees is negligible.

The specific objectives of this study were

(I) to verify the "nurse-tree effect" of the exotic tree plantations in comparison with the natural forest,

(II) to characterize the different light conditions on the basis of daily and seasonal patterns of PAR with regard to photosynthetic carbon uptake by the *P. falcatus* saplings,

(III) to examine the effects of other environmental variables on photosynthesis, and

(IV) to get insight in the water relations of the saplings in comparison to those of the shelter-trees.

Research plots were established in the natural forest as control and in a *Pinus patula* and a *Eucalyptus saligna* plantation. Ecological and physiological traits were recorded during dry and wet seasons over a period of 2 years and finally correlated with growth of the saplings.

1.6 Outreach of the study

In the Munessa forest the plantations are harvested by clear-felling. Whereas *Cupressus lusitanica* produces a huge amount of viable seeds from which the next generation of the plantation develops, *Pinus patula* and *Eucalyptus forests*, although ample producing cones and fruits, respectively, must be replanted, because germination of the seeds is poor. According to the available information regular rotation between the tree species after clear-felling of a plantation is not common. Taking advantage of the "nurse-tree effect", rotation would be possible between the exotic monoculture and a *Podocarpus* forest, which contains also some other indigenous broadleaf woody species. Up to the present time such rotation, depending on accidental seed input, may not be worthwhile from the viewpoint of forestry. However, allowing small groves of *Podocarpus* in exotic tree plantations would back up survival of the valuable indigenous tree species in the region while simultaneously maintain a source of viable seeds for a systematic rotation between the exotic and the indigenous species. Such mode of forest management may

greatly profit from the shelter-tree effect by which growth of *Podocarpus* juveniles is considerably accelerated.

Podocarpus falcatus is in great demand because of its straight stem and the quality of its wood which is higher than that of *Pinus patula*. Growth of young trees is relatively fast and the trees must be harvested before the onset of the differential activity of the cambium which results in the typical peripheral strands of old *Podocarpus* trees (Figure 1). The only disadvantage of this kind of forest management is the harvest of the shelter-trees which must be performed in a way by which the *Podocarpus* saplings are not heavily damaged. This is not a problem in the *Eucalyptus* plantation which is anyway coppiced from time to time, but may be a problem in a *Pinus* plantation. However, also there the economic surplus profit should balance the higher costs for harvesting.

2 Material and methods

2.1 Study area

Ethiopia at the “Horn of Africa” (Figure 3 A) is bordered by four dry countries, namely Eritrea in the North, Djibouti and Somalia in the East, Kenya in the South whereas in the West a humid area continues into the Sudan. Ethiopia’s size is about 1.1 million km², and it is inhabited by about 70 million people (FAO 2007). The topography is remarkably diverse, ranging from 120 m below sea level in the Danakil depression to mountainous regions well above 4000 m a.s.l. in the northern Semien and the southern Bale Mountains. Two-thirds of the land area are upland plateaus, and 50% of the country is above 1200 m a.s.l. The highland complex of mountains and plateaus is incised by the Great Rift Valley, which extends from the southwest to northeast of the country. As a consequence of its geographical position and its topology, Ethiopia’s landscapes comprise several climate regions and ecological zones: Deserts along the eastern border, tropical forest in the southwest and large afromontane and afroalpine regions in the northern and the south-eastern parts of the country (Figure 3 B).

The present study was realized in the Munessa-Shashamene Forest (7°13’ N 38°37’ E), which is a montainous area in the Arsi region on the eastern escarpment of the central Ethiopian Rift Valley, with an altitudinal range of the forest between 1900 and 3200 m a.s.l. The area of about 23,000 ha (Silvanova 1996) comprises patches of natural forest, a semi-dry evergreen afromontane forest, and plantations of cypress (*Cupressus lusitanica*), eucalypts (mainly *Eucalyptus saligna* and *globulus*) and pines (*Pinus patula*), and small crop fields and pastures. The tree density of the exotic plantations starts with approximately 1600 - 2500 trees per hectare; after thinning a final tree density of 500 - 600 trees per hectare remains.

The whole area is under the administration and management of the Munessa-Shashamene Integrated State Forestry Development and Utilization Project. The investigated plots of the present study are located in an area, locally known as “Kuke”, of 2280 m altitude. Kuke is a forest clearing where a research station has been established in 2004 (Figure 3 C).

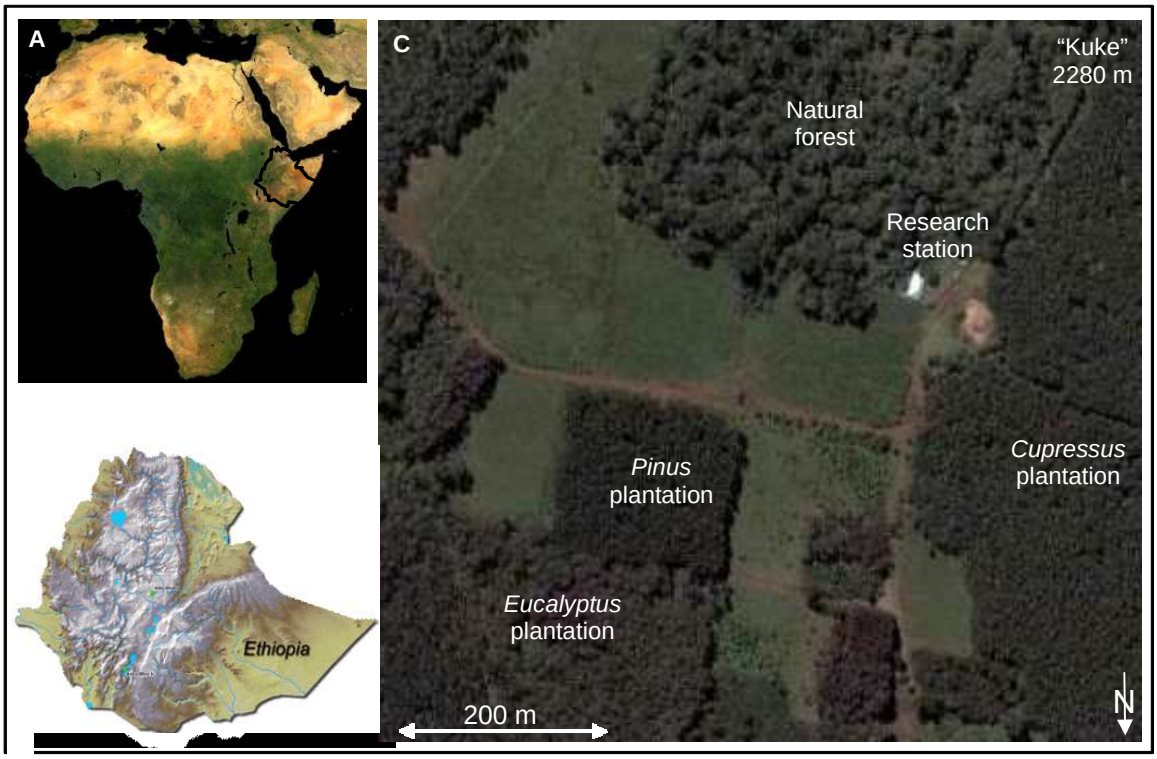

Figure 3: Ethiopia and the location of the study area. A: Map of Africa with Ethiopia (black hemmed) (satellite orthographic map: NASA), B: physical map of Ethiopia, central Ethiopian rift valley (Arsi region) marked by a black rectangle (satellite map Ethiopia: Wikimedia), C: Satellite image of the research area "Kuke" in the Munessa-Shashamene Forest, with natural forest and plantations of exotic tree species (Google Earth). Due to the camera angle of the image north is oriented to the lower side of the picture.

2.2 Climate of the research area

The reference climate station at Kuke was established in 2001 on the clearing close to the research station. The average annual rainfall is 1144 mm and the mean annual temperature is 15 ℃, both recorded from 2001 to 20 09 (Figure 4).

In 2006, when most measurements were made, annual rainfall (1413 mm) was higher than the average from 2001 to 2009 (1144 mm, Figure 4). The small rains came early in that year (March and April) and continued into the main rainy season from August to October. Also the amount of precipitation in the main rainy season was considerable higher than the annual average, with a maximum in July (296 mm *vs*. an average of 179 mm). Irrespective of the heavy rainfall in 2006, the annual mean of the air temperature (measured 2 m above ground level) did not differ from the eight years average.

Monthly averages and daily courses of important microclimate parameters are shown together with other data in the results section.

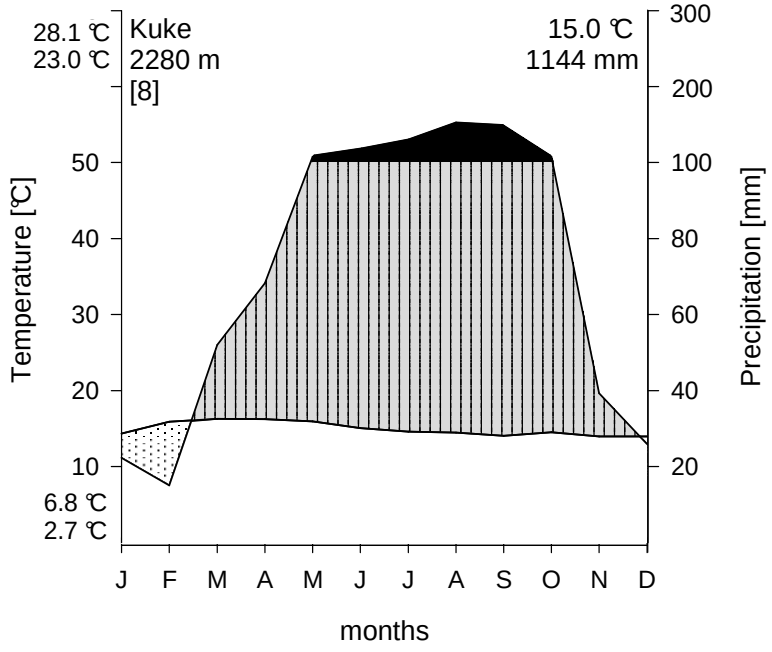

Figure 4: Walter-type climate diagram of the research area (eight year averages 2001 to 2009 at Kuke field station).

2.3 Geology and soils

The study area is a part of the great lake region of the main Ethiopian Rift Valley, situated east of the three great lakes Langano, Shalla and Abiata. The crests of the mountains of the eastern escarpment range between 3200 and 4000 m altitude. Like most parts of the Ethiopian Rift Valley, the bedrock of this upland consists of volcanic material from the Pliocene to early Pleistocene. Most of the bedrock can be affiliated with the trachytes (Benvenuti et al. 2002).

The soils of the study area at 2280 m a.s.l. were classified as Mollic Nitisols according to the World Reference Base of Soil Resources (WRB 2007). They are brownish to reddish, fine-textured but well drained with a high percentage of clay (over 50%) (Fritzsche et al. 2007). They are rich in nutrients, except phosphate and the upper horizons are slightly acidic (pH 6.3) (Fritzsche et al. 2007). More details of the soils in the Munessa-Shashamene region are given in related studies by soil scientists working in this region (Fritzsche et al. 2006; Fritzsche et al. 2007; Freier et al. 2010).

2.4 Investigated trees

2.4.1 *Podocarpus falcatus*

Podocarpus falcatus (Thunb.) R. Br. ex Mirb. is the dominant indigenous tree species in the afromontane Munessa-Shashamene Forest. It is an evergreen gymnosperm and belongs to the Podocarpaceae (Friis 1992). In the research area it grows up to 45 m high, with a corresponding stem diameter of 2 m. Its pale grey or brown bark, produces flakes of long irregular rectangles (Beentje 1994). The leaves are narrow, shiny dark green, 2 - 6 cm long, gradually tapering towards both ends; young leaves are larger and brighter giving a green flush (Bekele-Tesemma et al. 1993). *P. falcatus* is a tap root species (Fritzsche et al. 2006). Seeds of *Podocarpus* are dispersed mainly by birds and wildlife (Teketay 2011).

P. falcatus is found at altitudes between 1500 and 2600 m a.s.l., and in areas with an annual rainfall between 700 and 1500 mm and an average temperature between 15 and 20 °C (Friis 1992). It is native to Ethiopia, Burun di, Democratic Republic of Congo, Kenya, Lesotho, Malawi, Mozambique, Rwanda, South Africa, Sudan, Tanzania, and Uganda (Teketay 2011)

Termed the “East African yellow-wood” it produces a high-class softwood and is therefore used for many purposes like timber, furniture and handicrafts, while less valuable parts serve as firewood. Oil from the seeds is used for medical purposes.

2.4.2 *Pinus patula*

In the research area *Pinus patula* (Schldl. et Cham.), a member of the Pinaceae from Mexico, grows about 35 m high reaching a maximum diameter at breast height of 1.2 m. The bole is straight and cylindrical, rarely forked. The leaves grow in fascicles of 3 and are 15 to 25 cm long (Orwa et al. 2009). The bark of *P. patula* is characteristically reddish-orange in young trees and grey-brown and vertically ridged in older trees (Bekele-Tesemma et al. 1993). It is planted in an altitudinal range between 1000 and 3000 m a.s.l. and requires annual rainfall between 1000 and 2000 mm and a moderate temperature (Orwa et al. 2009).

Pinus patula was first introduced to South Africa in 1907 (Nyoka 2003) and was mentioned in Ethiopia at the turn of the 20th century (Nino 2009).

P. patula is a fast growing tree, its wood is suitable for timber, paper and firewood (Bekele-Tesemma et al. 1993).

2.4.3 *Eucalyptus saligna*

Eucalyptus saligna (Smith) from the Myrtaceae is a large evergreen tree, in Ethiopia usually 40 - 50 m high, but can reach 60 - 70 m, with a straight trunk and a stem diameter of up to 2 m (Bekele-Tesemma et al. 1993). The bark on old trunks is grey to brownish, rough with thick ridges and peeling in stripes. The leaves are up to 20 cm and 3 cm wide, pointed and curved. The colour of the upper side is silvery to green, the lower side is pale green (Bekele-Tesemma et al. 1993).

E. saligna is a fast growing and light demanding species which is adapted to subtropical climates with dry seasons of not more than 4 months (Orwa et al. 2009). Its altitudinal range is from sea level to 3100 m. It performs best on sites with 1400 to 1600 mm rainfall (Pohjonen and Pukkala 1990). *E. saligna* is highly suited for short-rotation plantations, and coppicing is recommended every 6 to 10 years for the production of firewood and pulpwood (Orwa et al. 2009), but due to the straight growth of the uncoppiced tree, it is sought for poles and pylons production (Pohjonen and Pukkala 1990). *E. saligna* is native to Australia, but grows successfully in plantations in the tropics and subtropics all over the world. *Eucalyptus* was introduced to Ethiopia at the end of the 19th century to accommodate the high demand of firewood of the growing population of Addis Ababa (Pohjonen and Pukkala 1990). Today, over half a million hectares of *Eucalyptus* plantations are established in Ethiopia (Dessie and Erkossa 2011).

2.5 Research sites and plots

In the three different forest types (natural forest, *Pinus* plantation and *Eucalyptus* plantation, all at 2280 m a.s.l., see Figure 3), sites were selected where several *Podocarpus* saplings grew in vicinity and under the typical canopy of the so-called “nurse-trees”. The situation in the selected plantation plots was artificial with regard to the density and distance of the “nurse-trees” but natural as far as the location, distance and age of the saplings were concerned. In the evergreen natural forest, the canopy was composed of *Podocarpus falcatus* and other broadleaf evergreens, mainly *Syzygium guineense*. The density of the saplings in the natural forest was smaller than in the plantations. Therefore two plots were selected in the natural forest (Plot 1a and 1b, Figure 5), one with a nurse-tree situation of one adult *Podocarpus* tree and five *P. falcatus* saplings, and the other with three medium size *Podocarpus* trees (Table 1 a). The second plot was already under investigation in the previous project phase. Wooden

scaffolds were established to reach the lower parts of the crowns of the “nurse-trees”. The distance of the microclimate stations on the scaffolds to the reference climate station at the research station was small allowing comparison of climate variables.

The three plots presented in Figure 8 were fenced with palisades and equipped with wooden scaffolds (10, 11 and 12 m high) which were constructed by local craftsmen on the spot. Microclimate stations were mounted on the scaffolds as described in detail in chapter 2.6. for recording sub-canopy climate variables. The horizontal distances between the plots were 350 m (natural forest - *Pinus* plantation) and 150 m (*Pinus* plantation - *Eucalyptus* plantation), respectively (Figure 3 C).

Figure 5: A: Natural forest with medium size *Podocarpus falcatus* (centre) and B: *Podocarpus* sapling (with red tape) in the natural forest in the plot 1a.

In the *Pinus* plantation, five 40-year old *Pinus patula* trees and 11 *Podocarpus falcatus* saplings grew on the selected plot (Figure 6, Table 1 b). In the *Eucalyptus* plantation, ten *Eucalyptus saligna* trees and seven *Podocarpus falcatus* saplings were selected, but because of the wider distance between the *Eucalyptus* “nurse-trees” only five *Eucalyptus saligna* adults and three *Podocarpus falcatus* saplings were enclosed in a fence (Figure 7, Table 1 c). The species composition and exact structure of the research plots is given in detail under chapter 2.5.1.

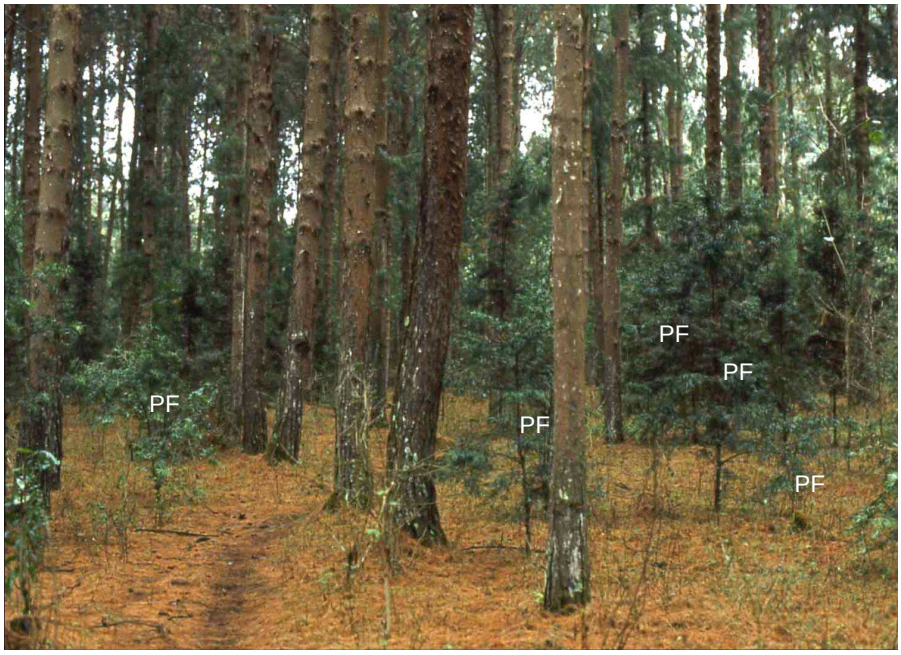

Figure 6: Understorey of an about 40 years old *Pinus patula* plantation with many *Podocarpus* saplings (PF).

Figure 7: View into an *Eucalyptus saligna* plantation with 3 *Podocarpus* saplings (PF) growing in the understorey.

Table 1: Sites and investigated trees as well as the performed measurements a) in the natural forest, b) in the *Pinus* plantation, and c) in the *Eucalyptus* plantation. Investigated saplings are typed bold.

a)

Natural forest	**Species**	**Label**	**Dbh [cm]**	**Height [m]**	**Measurements**
Plot 1a	*P. falcatus* (nurse-tree)	P1	21.3	16.5	Porometry, sap flow, growth
	***P. falcatus* sapling**	**NF P2**	1.6	1.8	Porometry, growth
	***P. falcatus* sapling**	**NF P3**	2.7	2.3	Porometry, growth
	***P. falcatus* sapling**	**NF P4**	4.9	4.7	Porometry, growth
	***P. falcatus* sapling**	**NF P5**	1.8	1.6	Porometry, growth
	***P. falcatus* sapling**	**NF P6**	2.6	2.2	Porometry, growth
Plot 1b	*P. falcatus*	P2	22.2	12.6	Sap flow, growth
	P. falcatus	P3	8.6	7.6	Sap flow, growth
	P. falcatus	P4	10.8	9.3	Sap flow, growth

b)

***Pinus* plantation**	**Species**	**Label**	**Dbh [cm]**	**Height [m]**	**Measurements**
Plot 2	*P. patula* (nurse-tree)	Pin 1	28.2	28.9	Porometry, sap flow
	P. patula (nurse-tree)	Pin 2	34.8	39.7	Sap flow, growth
	P. patula (nurse-tree)	Pin 3	40.8	35.1	Growth
	P. patula (nurse-tree)	Pin 4	24.9	32.8	Porometry, growth
	P. patula (nurse-tree)	Pin 5	22.6	23.5	Growth
	P. patula (nurse-tree)	Pin 6	20.1	23.3	Sap Flow, Growth
	***P. falcatus* sapling**	**Pin P1**	4.4	3.6	Porometry, sap flow, growth
	***P. falcatus* sapling**	**Pin P2**	2.4	2.7	Porometry, growth
	***P. falcatus* sapling**	**Pin P3**	3.1	3.2	Porometry, growth
	***P. falcatus* sapling**	**Pin P4**	2.7	2.4	Porometry, growth
	***P. falcatus* sapling**	**Pin P5**	2.0	2.6	Porometry, growth
	***P. falcatus* sapling**	**Pin P6**	-	0.7	Growth
	***P. falcatus* sapling**	**Pin P7**	1.7	1.9	Growth
	***P. falcatus* sapling**	**Pin P8**	2.4	3.0	Porometry, growth
	***P. falcatus* sapling**	**Pin P9**	2.0	2.2	Porometry, growth
	***P. falcatus* sapling**	**Pin P10**	0.9	1.5	Porometry, growth
	***P. falcatus* sapling**	**Pin P11**	-	1.1	Growth

c)

Eucalyptus **plantation**	**Species**	**Label**	**dbh [cm]**	**Height [m]**	**Measurements**
Plot 3	*E. saligna* (nurse-tree)	E1	16.8	24.5	Porometry, sap flow, growth
	E. saligna (nurse-tree)	E2	18.2	26.0	Sap flow, growth
	E. saligna (nurse-tree)	E3	34.0	39.5	Sap flow, growth
	E. saligna (nurse-tree)	E4	20.5	22.1	Growth
	E. saligna (nurse-tree)	E5	11.4	12.6	Growth
	E. saligna (nurse-tree)	E6	15.3	19.1	Growth
	E. saligna (nurse-tree)	E7	22.3	35.1	Growth
	E. saligna (nurse-tree)	E8	41.6	40.7	Growth
	E. saligna (nurse-tree)	E9	15.7	17.8	Sap flow, growth
	E. saligna (nurse-tree)	E10	11.0	20.1	Sap flow, growth
	***P. falcatus* sapling**	**E P1**	8.1	6.1	Porometry, Sap flow, growth
	***P. falcatus* sapling**	**E P2**	6.6	6.2	Porometry, growth,
	***P. falcatus* sapling**	**E P3**	5.1	5.3	Porometry, growth
	***P. falcatus* sapling**	**E P4**	8.1	7.1	Growth
	***P. falcatus* sapling**	**E P5**	-	1.3	Growth
	***P. falcatus* sapling**	**E P6**	8.9	9.0	Growth
	***P. falcatus* sapling**	**E P7**	1.8	2.5	Growth

2.5.1 The structure of the three forests, as reflected by the investigated plots

Young *P. falcatus* trees are less frequent in the natural forest (NF) and mostly not in good shape. The number of investigated saplings in the fenced plots in the natural forest was five at the beginning of the project in March 2005, however one died without visual impact (NF P2). Other tree species are also growing in the fenced plots, the most dominant being *Syzygium guineense* (Figure 8 A, T1 and T3). The coverage of the upper canopy as calculated from ArcView, added up to 99% of the plot area (Table 2). In contrast to the natural forest, many *P. falcatus* saplings were found in the *Pinus* plantation (PP, Figure 8 B), and most of them were in a good shape. The number of investigated saplings in the fenced *Pinus* plot was eleven. The canopy cover of the *Pinus patula* trees (calculated from the ArcView sketch) reached only 68% of the plot area (Table 2) showing nearly no overlapping of the crowns. In the *Eucalyptus* plantation, a couple of well growing *P. falcatus* juveniles had already reached a height of 9 m. There the number of investigated saplings was seven, but only three of them were inside the fenced plot (Figure 8 C). In the *Eucalyptus saligna* plot (ES) the cover of the

upper canopy was 72% (Table 2). The individual crowns of the *Eucalyptus saligna* trees were not as dense as the *Pinus* crowns but due to previous coppicing, the canopy had two layers which finally resulted in a patchy and partly very dense canopy.

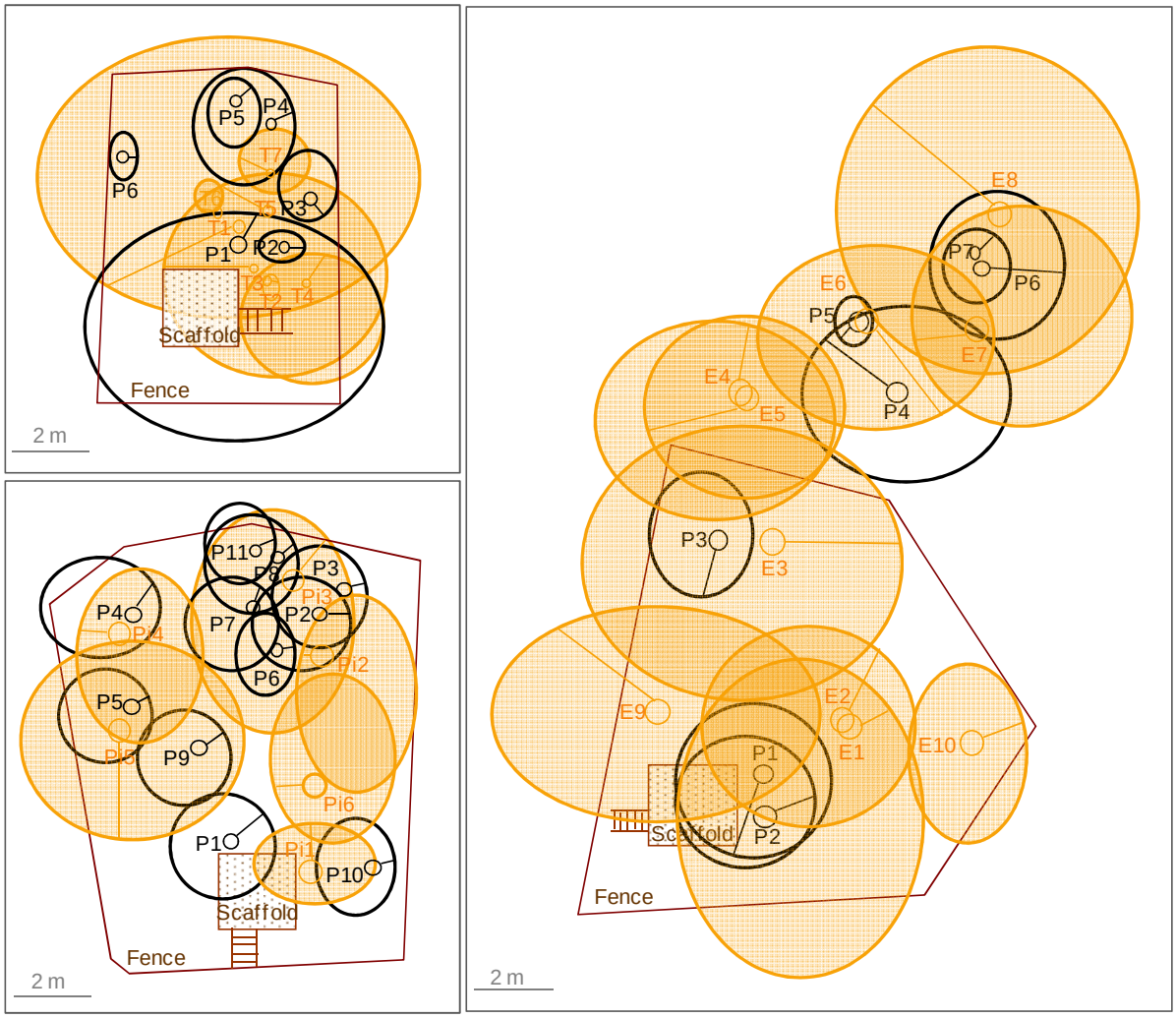

Figure 8: Structure of the investigated plots. Vertical projection of the crown areas of the investigated *Podocarpus falcatus* saplings/treelets (black circles) and of the shelter (orange circles) trees in the three plots. A: Plot in the natural forest, with an area of 52 m^2, B: Plot in the *Pinus* plantation, 102 m^2, C: Plot in the *Eucalyptus* plantation, 103 m^2; P: *Podocarpus falcatus*, Pi *Pinus patula*, E: *Eucalyptus saligna*, T other tree species; brown lines: fences.

Table 2: The canopy density of the three investigated plots. Percent cover was estimated from GIS Arcview data.

Site	Cover [%]
Natural forest	99
***Pinus* plantation**	68
***Eucalyptus* plantation**	72

2.5.2 Height, dbh and projected crown area of the saplings

All trees in the three different plots were identified and the exact diameter at breast height (dbh) was measured at the beginning of the study. The dbh of the *Podocarpus falcatus* saplings and of the "nurse-trees" (*Podocarpus falcatus*, *Eucalyptus saligna* and *Pinus patula*) were measured every 3 months. The heights of the *Podocarpus falcatus* saplings were measured every 3 months with a folding rule, the heights of the nurse-trees were measured at the beginning and the end of the study with a hypsometer (Forestor Vertex, Forestor Instrument AB, Sweden).

The extensions of the crowns of all nurse-trees and *Podocarpus falcatus* saplings were measured at the beginning and the end of the study (April 2005 and February 2007). Measurements were carried out in four directions (North, East, South and West) with a perpendicular and a measuring tape. From the results of the measurements a map of the plots with all trees and crowns was drawn and digitalized (GIS Arcview 3.1). With the program the size of the crowns was calculated and presented.

At the beginning of the study the investigated young *Podocarpus* trees in the natural forest were small with a diameter at breast height (dbh) ranging from 1.0 to 2.7 cm. Tree heights were between 2.1 and 2.5 m, except tree NF P4 with a dbh of 5.3 cm and a height of 4.7 m. In the *Pinus* plantation, the *Podocarpus* saplings were slightly taller. Dbh ranged from 1.5 to 5.2 cm, and heights from 0.8 to 5.1 m. Two *Podocarpus* saplings (Pin P6 and Pin P11) were too small for reaching breast height. In the *Eucalyptus* site, the young *Podocarpus* trees were again taller with dbh between 2.1 to 8.7 cm and heights from 1.4 to 9.7 m. One *Podocarpus* sapling (E P5) was too small for dbh measurement.

Projected crown areas of the *Podocarpus* saplings (Figure 8), calculated with GIS ArcView were small in the natural forest ranging from 1.1 to 2.1 m², except NF P4 with a

size of 7.1 m². In the *Pinus* site the crowns of the saplings ranged between 0.6 and 5.3 m² and in the *Eucalyptus* site from 1.0 to 16.2 m².

2.5.3 Height, dbh and projected crown area of the shelter-trees

The natural forest is dominated by *Podocarpus falcatus*, accompanied by *Syzygium guineense*, *Prunus africana* and *Croton macrostachyus*. In the plot only *Podocarpus falcatus* was considered a shelter-tree of the saplings. Compared to the shelter-trees in the plantations, the *Podocarpus* shelter-trees were much smaller, with a dbh between 10.4 and 21.6 cm and heights from 9.3 to 16.5 m. *Pinus patula* trees were between 23 and 40 m tall. Stem diameters of these trees ranged from 20.5 to 41.2 cm. In the *Eucalyptus* site, most of the trees had been coppiced once, only ES 3, ES 8 and ES 9 had their original size. Therefore, the diameters at breast height and the heights of the *Eucalyptus saligna* trees differed considerably. Their heights ranged from 12.6 m (coppiced tree) to 40.7 m (non-coppiced tree) and their dbh from 11.0 to 41.6 cm.
Crown areas of the shelter-trees had a wide range in all sites. The *Podocarpus falcatus* shelter-trees had crown projection areas between 6.7 and 31.7 m²; Crown areas of *Pinus patula* ranged from 5.3 to 25.9 m². The biggest crowns were those of the *Eucalyptus saligna* trees ranging from 6.9 to 44.5 m². Here, the great variation was due to the presence of coppiced and untreated trees.

2.6 Microclimate

The area's climate and the microclimates under the canopies of the shelter-trees were monitored with three climate stations.
The reference climate station (Metos, Pessl Instruments, Weiz, Austria) inside the compound of the research station measured the climate of the open area. Records were for relative humidity, air temperature, solar radiation, brightness, leaf wetness, wind speed, precipitation and soil temperature. The sensors were installed in 2.0 m height, the rain collector at 1.0 m height and the sensor for soil temperature at 20 cm depth. The station was running since 2001. The measuring interval by this station as well as of the sub-canopy microclimate stations was ten minutes and the values were averaged over one hour.

2.6.1 Sub-canopy microclimates

In order to investigate the sub-canopy microclimate provided by the “nurse-trees” two climate stations (Thies Clima, Adolf Thies GmbH & Co.KG, Göttingen, Germany), equipped with sensors for relative humidity, air temperature, solar radiation, and photosynthetic active radiation were mounted on the scaffolds. The rain gauge for measuring throughfall was placed next to the scaffold 1 m above ground. In the other microclimate station throughfall was measured with a tipping-bucket rain gauge and a HOBO Event Logger (Onset Computer Corporation, Bourne, MA, USA). The station in the natural forest was operated permanently; the other climate station was periodically used in the *Pinus* and the *Eucalyptus* plots. The sensors were installed 1.2 (throughfall collector) and 1.5 m (PAR, global radiation, air temperature and relative humidity) above the ground and at different heights on the scaffolds (Figure 9, Figure 10). Another PAR sensor was mounted on the scaffold at 7.0 m, the remaining sensors (PAR, global radiation, air temperature and relative humidity were exposed around the top platform of the scaffold between 11 and 13 m, depending on the height of the scaffold.

Electricity was provided from 3 solar panels which were mounted on outriggers from the top of the scaffolds.

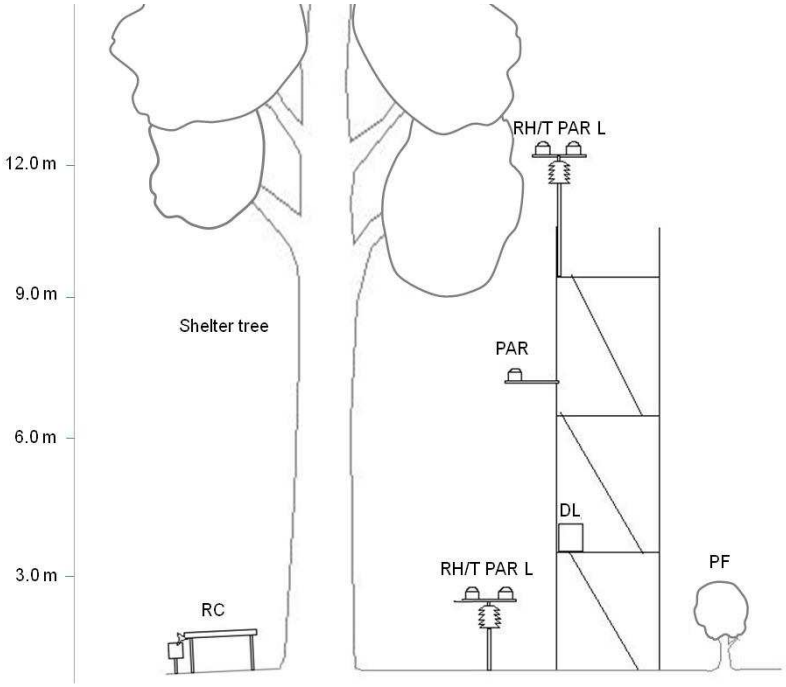

Figure 9: Sketch of microclimate station mounted on the scaffold and the position of the sensors. RH/T sensors for relative humidity and air temperature, PAR sensor, L global radiation sensor, RC throughfall collector, DL data logger, PF *Podocarpus falcatus* sapling.

Figure 10: A: PAR, global radiation, temperature and relative humidity sensors on top of the scaffolds, B Understorey station with sensors for PAR, global radiation, temperature, relative humidity, and throughfall collector; C scaffold in the *Eucalyptus* plantation.

2.7 Measurement of sap flow

Whole-tree transpiration can be measured via quantification of the sap flow through the xylem. Commonly the heat dissipation method (Granier 1985) is used for this purpose.

2.7.1 Heat dissipation method (Granier)

The measuring unit consists of two sensors which are inserted radially in a vertical distance of 10 cm in the stem. The Design of both sensors is identical with a length of 20 mm or 40 mm and a diameter of 2 mm. They consist of a constantan heating coil at the tip and a copper-constantan thermostat relay. The upper sensor is heated with constant current of 120 mA, the lower one is used as a reference and has the same temperature as the ambient wood. Water flow in the stem cools the heated sensor. The change of its temperature depends on the velocity water flux, and is registered by the data logger as a voltage fluctuation (40 µV = 1 ℃). Because it is o nly the upper sensor which is (heated

and) cooled, the lowest sap flow rates are reflected by the maximum temperature difference (Figure 11 A).

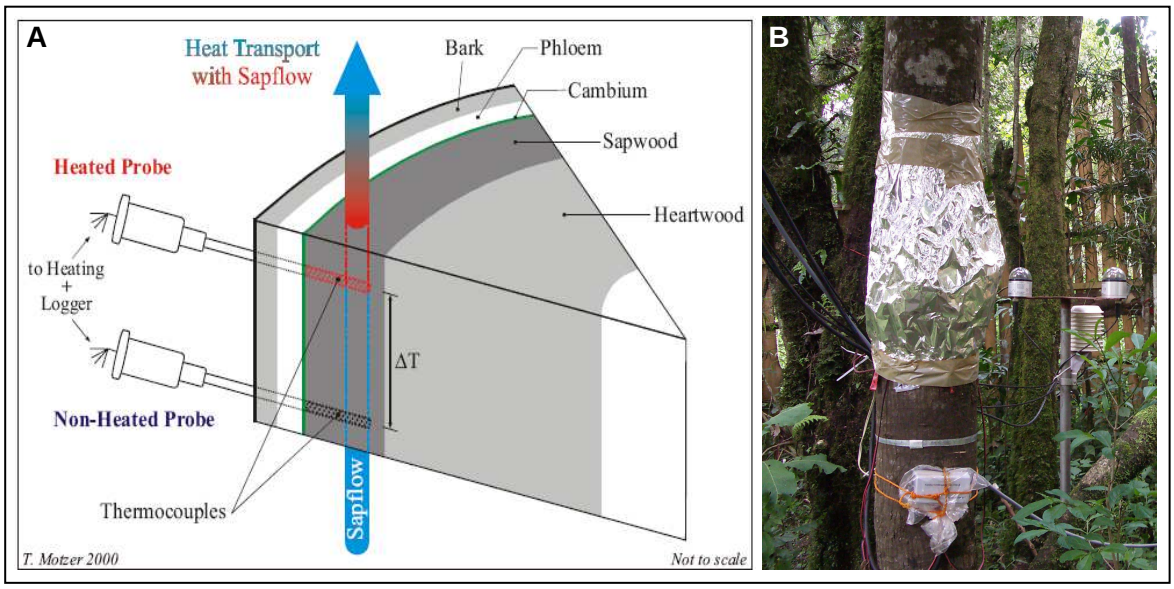

Figure 11: A: Principle of sap flow measurements with the Granier method (Motzer 2003), B Sap flow measurement in the natural forest on a *Podocarpus falcatus* (nurse-tree) with radiation protection of aluminium foil and constant power supply, in the background the sensors of the microclimate station.

2.7.2 Sap flow measurement

Sap flow measurements were performed between March 2005 and February 2007. Four *Podocarpus* trees in the natural forest were investigated for 101 days, 64 days in the rainy season and 39 in the dry season. In the *Pinus* site, measurements were carried out on three *Pinus* nurse-trees and one *Podocarpus* sapling on 21 days, 18 days in the rainy season and 3 days in the dry season. In the *Eucalyptus* plantation, sap flow was measured on 9 days in the rainy season and 3 days in the dry season, in total 12 days, on five *Eucalyptus* nurse-trees and one *Podocarpus* sapling. Each tree was equipped with three pairs of sensors (Heinz Kauper, Bayreuth, Germany), except the *Podocarpus* sapling in the *Pinus* site which was too small in circumference; only one pair of sensors was installed there. The three pairs of sensors were placed equidistantly on the circumference of the stem.

For the installation of the sensors two holes of 2.1 mm width were drilled in the stem at breast height in a vertical distance of 10 cm. The holes were lined with aluminium tubes to protect the sensors and to warrant optimal heat exchange between the sensor and the surrounding wood. Additionally silicone grease was used to improve heat transition

between the sensor and the aluminium tube. The sensors were connected to a power distribution box (Electronics workshop of the University of Bayreuth), a constant power supply (lead acid battery and solar panels, Conrad Electronic, Hirschau, Germany) and a data logger (DL2E, Delta-T Devices, Cambridge, UK). Finally sensors were air-tight sealed with wax (Lauril Wundwachs, W. Neudorff GmbH, Emmerthal, Germany) and wrapped with several layers of aluminium foil to protect the probes against rain and heating by solar radiation (Figure 11 B).
Measurements were taken every 30 seconds, and every ten minutes the averages of 20 readings were stored in the data logger.

2.7.3 Calculation of sap flow

Calculation of sap flow was via sap flow density as suggested by Granier (Granier 1985) (Equations 1 and 2).

Sap flux density

$$J_S = \alpha \cdot k^b \quad [ml \cdot cm^{-2} \cdot min^{-1}] \qquad (1)$$

J_S = Sap flow density
α = Coefficient (0.714)
k = relation of heated and unheated probe
b = Scaling exponent (1.231)

$$k = \left(\frac{\Delta T_M}{\Delta T} - 1 \right) \qquad (2)$$

ΔT_M = Maximum temperature difference between heated and reference probe at sap flow = 0
ΔT = Temperature difference between heated and reference probe

Sap flow is calculated by equation 3:

$$SF = J_S \cdot A_{SW} \quad [ml \cdot min^{-1}] \qquad (3)$$

SF = Sap flow
J_S = Sap flow density
A_{SW} = Sap wood area

2.7.4 Identification of sap wood area

Sap flow density relates to a normalized area (commonly 1 cm^2). In order to calculate the actual sap flux, sap flow density must be multiplied with the conducting area of the stem, the so-called soft- or sap wood. In the heart- or hardwood, the conducting elements of the xylem are plugged by tyloses and thus cannot contribute to water transport. For the determination of the conducting area of the stems, wood samples were taken with an increment borer (Suunto Oy, Vaanta, Finland). To leave the investigated trees undamaged wood samples were taken from equivalent trees in the neighbourhood. In the drill cores, the borderline between the heart- and the sap wood could be microscopically recognized for *Eucalyptus* by the lack or presence of tyloses. For the conifers, the different colour (*Podocarpus falcatus*) or the wet and the dry part (*Pinus patula*) of the sample delimited the sap wood area from the heart-wood.

The sap wood area was simply calculated (equation 4) by

$$A_{SW} = A_{CS} - A_{HW} \qquad (4)$$

A_{SW} = Sap wood area
A_{CS} = Cross section area
A_{HW} = Heart wood area

From the ratio between sap wood area and cross section area of conspecific trees of different size a regression line was calculated, from which the sap wood area of other than the examined individuals could be estimated.

2.7.5 Calibration of sap flow sensors

Granier (Granier 1985) has published a calibration curve for the coefficient K of sensor pair versus actual sap flow density. While K-values for several trees fit to the calibration curve, no data were available for *Podocarpus falcatus*. Therefore a calibration experiment was carried out with a *P. falcatus* tree from the natural forest with a height of 9.5 m and a dbh of 10.2 cm. The stem of the tree was equipped with three sap flow sensors for equilibration. After three days the stem was cut 50 cm below and above the inserted probes. In the laboratory the sensors were activated by electrical power and connected to a data logger, and the section of the stem was firmly fixed upside down in a vertical position. On the new top, a tube with the same diameter was mounted, sealed

with silicone and filled with water. At the lower end of the stem section water flux out of the stem was recorded with a balance while the data logger registered the temperature difference between the sensors. From both datasets a regression was produced (Figure 12).

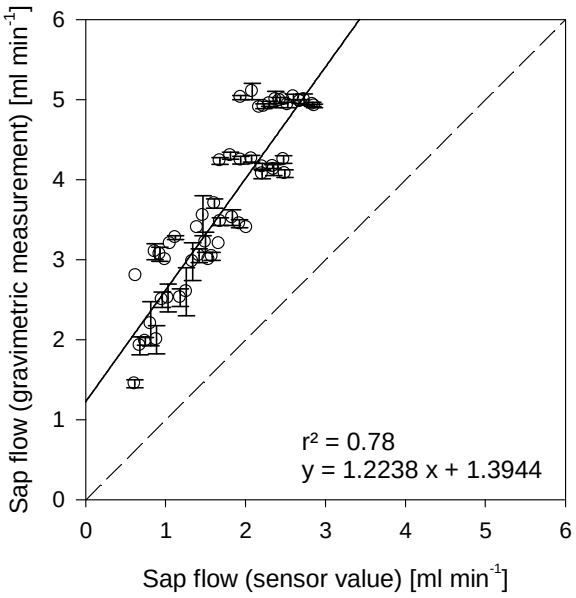

Figure 12: Calibration of the Granier sap flow sensors for *Podocarpus* (dbh 9.5 cm). Dashed line: theoretical correlation according to Granier (Granier 1985).

2.8 Gas exchange

CO_2 net gas exchange was measured with a Walz porometer.

2.8.1 Principle of the Walz porometer

With the Walz porometer (GFS-3000, Heinz Walz GmbH, Effeltrich, Germany) gas exchange (CO_2, H_2O) of a leaf was measured in various modes, under natural, ambiental conditions, at artificial light intensities (light response curve), at preset CO_2 concentrations and of the darkened leaf (dark respiration). Since the Walz porometer or the similar LICOR instrument are used worldwide, a detailed description of its function will not be presented here. It should, however, be mentioned that with the porometer also the stomatal conductance and from the simultaneously recorded relative humidity or VPD and the air (or leaf) temperature, transpiration can be determined. A sketch of the construction and functioning of the Walz porometer is provided in Figure 13 A.

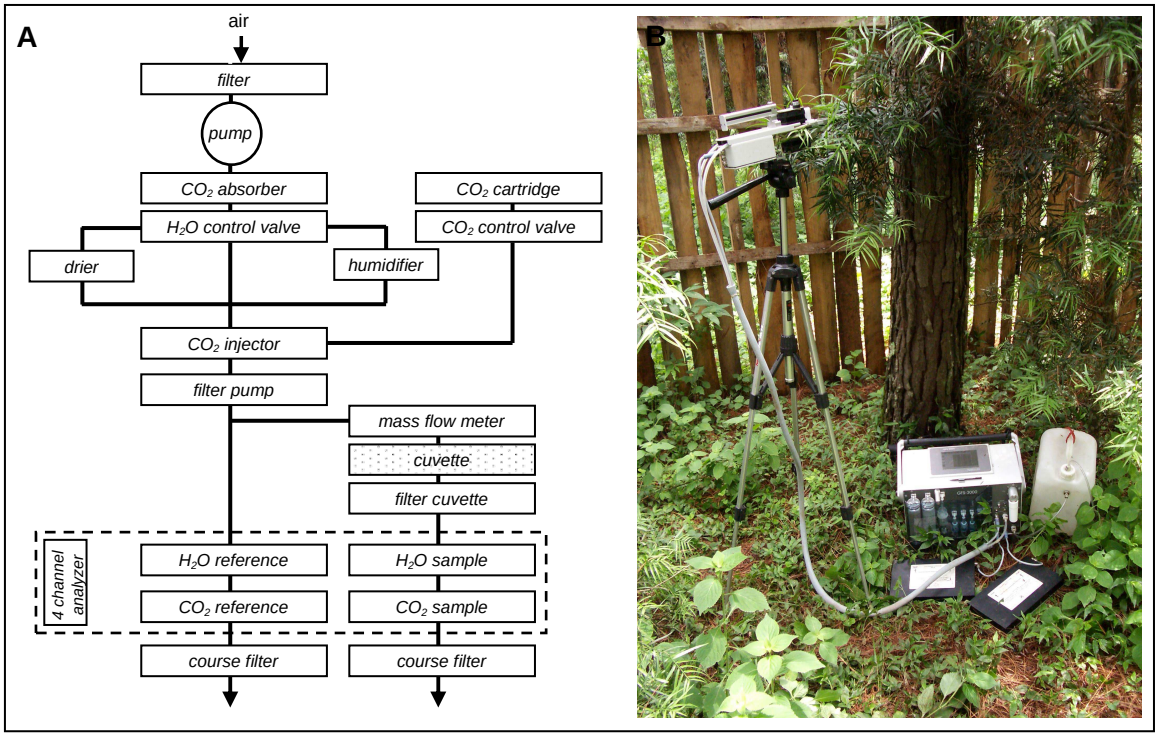

Figure 13: A: Principle of the GFS-3000 porometer in the CO_2 controlled mode (Walz 2005, modified sketch), B: Measurement of photosynthesis of a *Podocarpus falcatus* sapling in the *Pinus* plot.

2.8.2 Measurement of photosynthesis

Photosynthesis was measured in three campaigns from September to December 2005 (end of rainy season and early dry season), from February to July 2006 (end of dry season and rainy season) and from November 2006 to February 2007 (dry season after an extended rainy season). Because one single *Podocarpus* leaf is too narrow to fill the opening of the sensor head, 3 to 4 leaves, while still attached to the twig were put together side by side to fill the aperture of the cuvette. Turning the twig as far as possible in its natural position, the arrangement was left for the entire measurement which commonly took the whole light-period of the day. Such daily courses of CO_2 net uptake by the leaves of the *Podocarpus* saplings and the simultaneously measured microclimatic parameters were recorded in the natural forest (5 saplings, 16 days), in the *Pinus* site (8 saplings, 22 days) and in the *Eucalyptus* site (3 saplings, 21 days). Photosynthesis of the “nurse-trees” was measured on 9 days in the natural forest (1 *Podocarpus falcatus*), on 13 days with the *Pinus* (2 trees), and on 6 days at the *Eucalyptus* site (1 *Eucalyptus saligna* tree). All measurements were performed in the dry and the rainy season.

In addition to the daily courses of photosynthetic CO_2 net uptake or respiratory release, also light and CO_2 saturation curves of photosynthesis were measured. For comparison, some *Podocarpus falcatus* trees growing outside a shelter were also measured. These trees grow in a young cypress plantation of which the trees were about 1 - 1.2 m high and thus lower than the *Podocarpus* sapling.

2.9 The δ ^{13}C isotope ratio

The measurement of the δ ^{13}C isotope ratio of plant material allows an assessment of the long-term water relations of the plant under the climatic conditions during the life-time of the respective plant organ. The theory of the ^{13}C discrimination analysis has been generally accepted (Farquhar et al. 1989). Higher values of the isotope ^{13}C indicate less stomatal resistance, i.e. generally moister ambiental conditions. A set of δ ^{13}C values enclose the values which are typical of C4- and C3-plants, respectively, indicating moister or drier long-term conditions.

Leaf samples for δ ^{13}C analysis were collected in July 2006 from three *Podocarpus* saplings and from three nurse-trees of each site. From all trees and saplings, old and young leaves from different parts of the crowns were sampled and dried. The δ ^{13}C isotope ratios were determined in the laboratory of the Isotope Biogeochemistry of the Bayreuth Centre for Ecology and Environmental Research with an isotope ratio mass spectrometer (IRMS, delta S, Finnigan MAT, Bremen, Germany). Carbon isotope ratios are expressed in relation to the PDB standard (Ehleringer et al. 1987).

Carbon isotope ratio:

$$\delta_s = \frac{R_s}{R_{st}} - 1 \qquad (5)$$

δ_s = δ ^{13}C ratio in the plant
R_s = δ ^{13}C Isotopic abundance in the plant
R_{st} = Molar abundance ration of the standard (^{13}C/^{12}C)

2.10 Statistical analysis

Statistical analyses of the data were performed with the software R version 2.9.0. (R Development Core Team 2009) Mainly tests on normal distribution of the data were performed (Shapiro-Wilk Test), but also linear mixed-effect models using the lme4 package (Bates 2005), factorial analysis of variance (ANOVA) and post-hoc separation of means with Scheffé's test were applied, too, and the significance of differences of means was investigated with Levene's test (t-test). Differences of the data were considered significant when $p < 0.05$.

3 Results

3.1 Growth

Growth of the saplings was periodically monitored over two years from March 2005 to February 2007. The average monthly relative growth rates (increments of the diameters) averaged over two years were 0.08, 0.30 and 0.09 mm per cm for the trees in the natural forest, the *Eucalyptus* and the *Pinus* site, respectively. Statistical analyses showed a significant difference in growth between the saplings in the *Pinus* plantation and the other two sites (*Pinus* plantation – natural forest: $\chi^2 = 3.71$, $p = 0.05$, *Pinus* plantation – *Eucalyptus* plantation: $\chi^2 = 7.21$, $p = 0.007$). The differences in growth rates between the *Podocarpus falcatus* saplings in the natural forest and the *Eucalyptus* plantation were statistically not significant (Figure 14). Surprisingly, significant differences between the growth rates during the dry and the rainy seasons could not be observed.

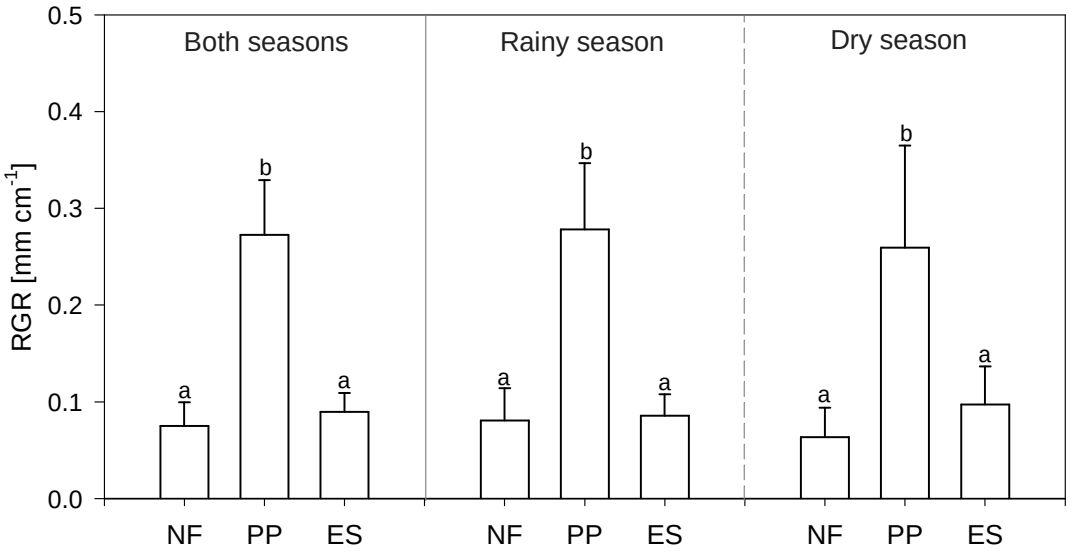

Figure 14: Monthly relative growth rates (radial growth at dbh) of *Podocarpus* saplings at the three sites measured over two years (April 2005 to March 2007). Different lower case letters indicate statistically significant differences. RGR was investigated with the linear mixed effect model, with the plots as fixed factors and the individual trees and numbers of measurements as random factors.

3.2 Soil-born factors of potential effects on growth

Investigations of the mycorrhiza of the trees (Wubet et al. 2003) showed that there is no sharing of mycorrhiza of the exotic trees with *Podocarpus*. Also investigations on site conditions and nutrient cycling in the soil (Fritzsche et al. 2006; Freier et al. 2010) showed that the conditions for the saplings in the plantations are not better compared to those of the natural forest. Since the plantations were in close vicinity to each other and to the natural forest, soil profiles were similar, except the organic layer of the top soil. Soil-born factors were therefore excluded as proximate causes of different growth rates.

3.3 Climate and sub-canopy microclimate of the plots

Due to the overall homogeneity of the soil structure and chemistry (Scheidegger et al. 2000; Fritzsche et al. 2006; Freier et al. 2010) differences in growth of the *Podocarpus* saplings should primarily results from different microclimates under the three different canopies of the exotic plantations and the natural forest. Therefore this chapter focuses on the different sub-canopy microclimates. Due to the availability of only 2 microclimate stations continuous readings are only for the reference and one microclimate station. The second microclimate station was periodically moved between the two plantation sites.

3.3.1 The effects of the different canopies on the sub-canopy microclimates

3.3.1.1 Temperature

Monthly means of the air temperature (1.5 – 2 m above ground) level fluctuated only slightly in the course of the year, as it is typical for tropical regions (Figure 15). An annual average temperature of 15.0 °C was calculate d from the data of the reference station at Kuke at 2280 m a.s.l. (Figure 4). Seasonal fluctuations did not exceed 2.0 °C. A clear correlation between the air temperatures and the seasonality of the precipitation could not be observed.

Differences in the monthly air temperatures between the three forest sites and the reference station were only seen in the dry season (October to March) when the sub-canopy air temperature in the natural forest was slightly lower (> 0.8 °C) than outside the forest. Between the plantations and the natural forest differences were more

pronounced with monthly means up to 1.8 ℃ higher in the *Pinus* and the *Eucalyptus* site, especially at the beginning of the dry seasons between November 2006 and January 2007 when the temperatures in the *Pinus* and *Eucalyptus* plantation reached even slightly higher values than the reference station.

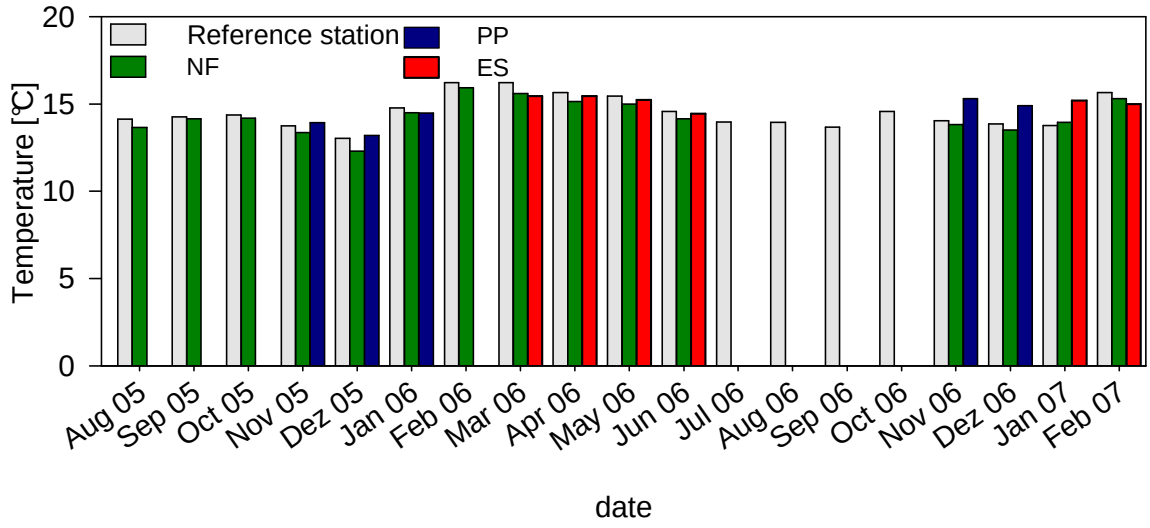

Figure 15: Monthly means of the air temperatures 1.5 m above ground in the three forest plots (NF: natural forest, ES: *Eucalyptus saligna* plantation and PP: *Pinus patula* plantation and of the reference station outside the forest (2 m). Due to the availability of only 2 microclimate stations continuous readings are only for the natural forest plot. The second microclimate station was started in November 2005 and was periodically moved between the 2 other sites. Thus, data sets from the plots in the *Pinus* and the *Eucalyptus* plantations are principally not continuous. Between July and October 2006, both microclimate stations in the forest sites had additionally technical problems.

3.3.1.2 Water vapour pressure deficit (VPD) and relative humidity (rH)

The annual course of the monthly means of vapour pressure deficit (VPD) (Figure 16) and relative humidity (rH) (Figure 17) showed contrasting patterns. Mean values of VPD inside the forest were higher most of the time compared to the reference station, only at the end of the dry and the beginning of the rainy season monthly means of VPD were higher outside the forest. Seasonal fluctuations were high, ranging from less than 1 hPa in the rainy season to mean values of 5.8 hPa outside the forest, and up to 6.4 hPa inside the forest (Figure 16). The comparison between the forest sites showed no significant differences between the natural forest and the *Eucalyptus* site and also compared to the reference station in both seasons, whereas the *Pinus* plantation was significantly drier (Figure 16, Table 3), with monthly means of VPD 0.9 to 1.8 hPa higher than the natural forest and 0.9 to 1.5 hPa higher than the reference station outside the forest.

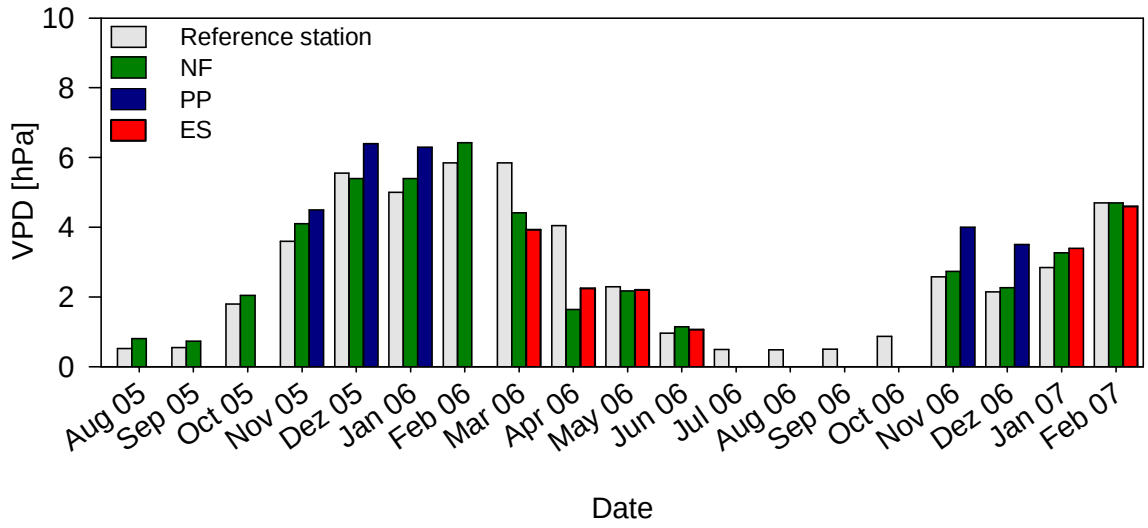

Figure 16: Monthly means of VPD (recorded 1.5 m above ground level) in the three forest plots (NF: natural forest, PP: *Pinus patula* plantation, ES: *Eucalyptus saligna* plantation) and of the reference station outside the forest (2 m above ground). With respect to gaps in the data sets refer to the legend of Figure 15.

The annual pattern of relative humidity (Figure 17) showed reciprocal seasonality. In the rainy season, monthly means did not differ significantly between the sites. Values were in general very high, especially during the rainy season, and sometimes higher inside than outside the forest. There were no obvious differences between the natural forest and the *Eucalyptus* plantation, data for the *Pinus* plantation are not available for the rainy season.

In the dry season, differences between the sites were more pronounced. In accordance with VPD, driest conditions were found in the *Pinus* plantation where monthly means of relative humidity dropped to 58%, which is even less than the lowest monthly mean outside the forest (63%). In the natural forest, the air was slightly moister (by 5%). The same holds in principle for the *Eucalyptus* plantation with a minimum of 73% at the end of the dry season 2007 when relative humidity under the *Eucalyptus* and the natural canopy equalled that of the reference station.

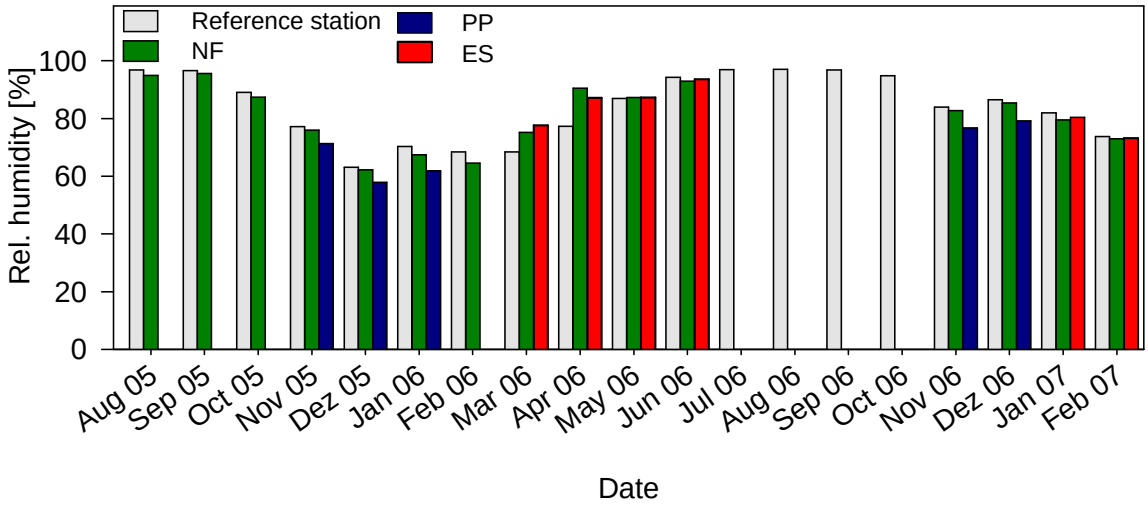

Figure 17: Monthly means of the relative humidity 1.5 m above ground level in the three forest plots (NF: natural forest, PP: *Pinus patula* plantation, ES *Eucalyptus saligna* plantation) and of the reference station at the research station (2 m above ground). With respect to the gaps in the data refer to the legend of Figure 15.

3.3.1.3 Throughfall

Annual precipitation of the reference station outside the forest was 1150 mm. The annual pattern showed a long rainy season from mid of March to October and a dry season between November and February (Figure 4). The annual course of throughfall in all three forest types (Figure 18, Table 3) reflected in principle the annual pattern of rainfall recorded by the reference station. Averaging over the 3 sites and the seasons, throughfall was around 43% of the precipitation, with clear differences between the seasons and depending on the intensity and duration of the rainfall events. During short showers, especially in the dry season, interception in the canopies and evaporation almost balanced the amount of precipitation and hardly any rain reached the ground level. In the natural forest, monthly throughfall ranged between 1 and 48% of the rainfall during the dry season, and between 30 and 77% in the rainy season. The corresponding monthly means in the *Pinus* site were 4 to 66% in the dry season, and 46 to 58% during the rains. In the *Eucalyptus* site, data are available only from the rainy season when mean throughfall was between 47 to 76% of the precipitation. Significant differences between the natural forest and the plantations could not be observed.

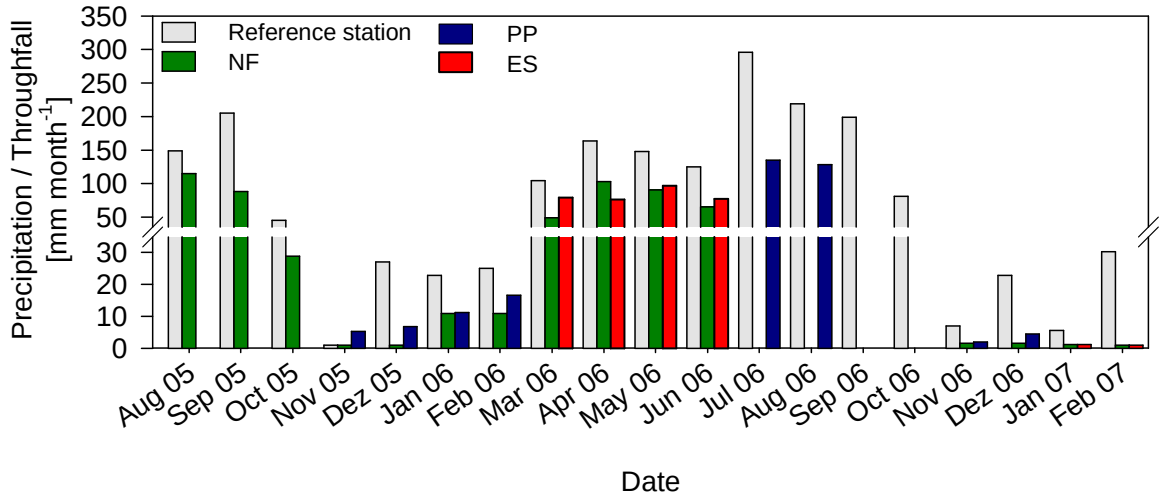

Figure 18: Monthly means of throughfall in the three forest types as compared to the (monthly) precipitation outside the forest. Between July and October 2006 (rainy season), the microclimate station in the natural forest (NF) had a technical problem and in September and October 2006 also the rain gauge of the second microclimate station which was started in November 2005, failed.

3.3.1.4 Photosynthetic active radiation (PAR)

Figure 19 shows the monthly averages of the mean daily sums of PAR outside the forest and in the three sites. Outside the forest, values for PAR were calculated from total solar radiation using the factor f = 0.46 (Rao 1984). Sub-canopy PAR was measured directly with PAR sensors. The monthly means of the reference station outside the forest were between 17.2 and 40.8 mol m^{-2} d^{-1}, whereas in the natural forest and the plantations, only 0.8 to 3.4% of the total irradiation reached the level of the saplings. Compared to the natural forest, mean values of PAR were approximately two times higher in the plantations. Seasonal differences of PAR on the individual sites were significant outside the forest, but not for PAR under the 3 canopies (Table 3).

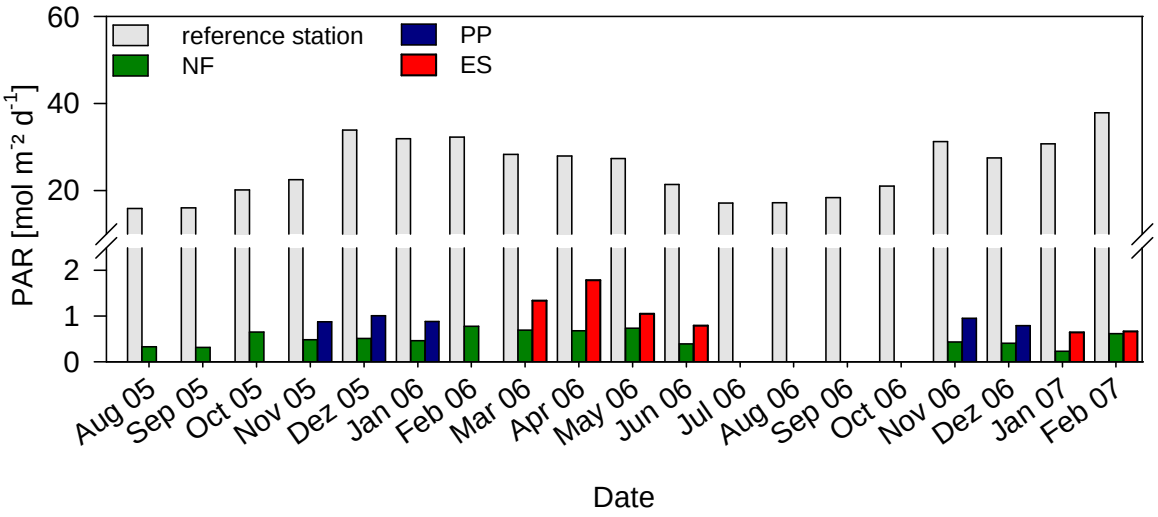

Figure 19: Monthly average of the daily sums of the solar radiation 1.5 m above ground level in the three forest plots and of the reference station outside the forest (2 m). For gaps in the data sets refer to the legend of Figure 15.

Table 3: Climate factors determined by the reference station outside the forest, and of the sub-canopy spaces of the three forest types. Numbers represent monthly means and standard errors. Data for Solar radiation, PAR, VPD, precipitation and throughfall are calculated from 19 months (reference station), 15 months (natural forest), 5 months (*Pinus* plantation) and 6 months (*Eucalyptus* plantation), respectively. Numbers in brackets show values of the reference station which directly correspond to the respective measuring periods. Lowercase letters indicate significant differences between seasons and sites.

	Reference station	Natural forest	*Pinus* plantation	*Eucalyptus* plantation
Solar radiation [mol m^{-2} d^{-1}]				
Rainy season	45.0 ±2.5[a]			
Dry season	72.0 ±1.5[b]			
PAR [mol m^{-2} d^{-1}]				
Rainy season	20.5 ± 1.1[a]	0.2 ± 0.01[c] (21.2 ± 2.6)	no data (20.5 ± 1.1)	1.0 ± 0.2[d] (24.4 ± 2.1)
Dry season	33.0 ± 0.7[b]	0.2 ± 0.01[c] (30.7 ± 1.9)	0.9 ± 0.03[d] (34.4 ± 0.9)	0.8 ± 0.2[d] (31.2 ± 1.0)
VPD [hPa]				
Rainy season	1.3 ± 0.4[a]	1.4 ± 0.3[a] (1.7 ± 0.6)	no data (1.3 ± 0.4)	1.8 ± 0.4[a] (2.9 ± 0.9)
Dry season	4.2 ± 0.5[b]	4.3 ± 0.4[b] (4.2 ± 0.5)	5.0 ± 0.7[c] (3.8 ± 0.7)	4.0 ± 0.1[b] (4.4 ± 0.9)
Precipitation [l $month^{-1}$] and Throughfall [%]				
Rainy season	148.6 ± 22.7[a]	53 ± 7[c]%	56 ± 4[c]%	54 ± 8[c]%
Dry season	27.2 ± 10.3[b]	34 ± 15[d]%	32 ± 6[d]%	no data

[1]Monthly means of PAR of the reference station are calculated from solar radiation using a conversion factor of f=0.46 (Rao 1984).

3.3.2 Vertical gradients in the sub-canopy microclimates summarized over the year

3.3.2.1 Temperature, relative humidity and VPD

The gradients of the components of the microclimate under the canopies of the shelter-trees between the lowest branches in 10 m (natural forest) or 12 m height (plantations) and the saplings level at 1.5 m height were recorded with the sensors on the scaffolds. Air temperature decreased by less than 1 °C (on average) towards the forest floor. Concomitantly, relative humidity increased up to 10% during the dry, and up to 5% during the rainy season. Accordingly, monthly means of VPD were always higher at 10 or 12 m compared to the values at saplings level. Differences were more pronounced in the rainy season when mean VPD values at the top of the scaffold were up to 40 and 50% higher compared to the saplings level in the *Eucalyptus* site and the natural forest, respectively. In the dry season, values of VPD were 27 and 20% lower at saplings level in the natural forest and the *Eucalyptus* plantation, respectively, and only 7% lower in the *Pinus* site, as compared to the lower side of the canopy.

3.3.2.2 Photosynthetic active radiation

The strongest decrease of PAR from the lower side of the canopy to the saplings level was observed in the natural forest where the mean daily sum of PAR was 3.5 times higher at the upper (0.7 mol m^{-2} d^{-1}) compared to the lower level (0.2 mol m^{-2} d^{-1}) (Figure 20). In the *Pinus* plantation, the decrease was less pronounced, as 56% (0.9 mol m^{-2} d^{-1}) of PAR measured immediately under the canopy (1.6 mol m^{-2} d^{-1}) reached the saplings. The respective decrease of PAR under the *Eucalyptus* canopy was in between the two gradients with 2.4 times higher values measured under the canopy (1.9 mol m^{-2} d^{-1}) compared to the saplings level (0.8 mol m^{-2} d^{-1}). It must be kept in mind that the canopy of the *Eucalyptus* plantation was in partly two-tiered, consisting of the crowns of the uncoppiced and of the young *Eucalyptus* trees that had regrown from the coppiced stumps. Beneath the old *Eucalyptus* individuals the irradiation was usually higher as there was only 1 crown. Due to this structure the canopy of the *Eucalyptus* forest was patchy and the gradient of PAR was not everywhere the same.

Nevertheless growth of the *Podocarpus* saplings under all three shelters lead them into a better light climate counteracted by a reduction of the relative humidity of the air. Since the gradients in temperature und VPD were less steep than that of PAR, the decrease in humidity did not outweigh the positive effect of the increasing light intensity.

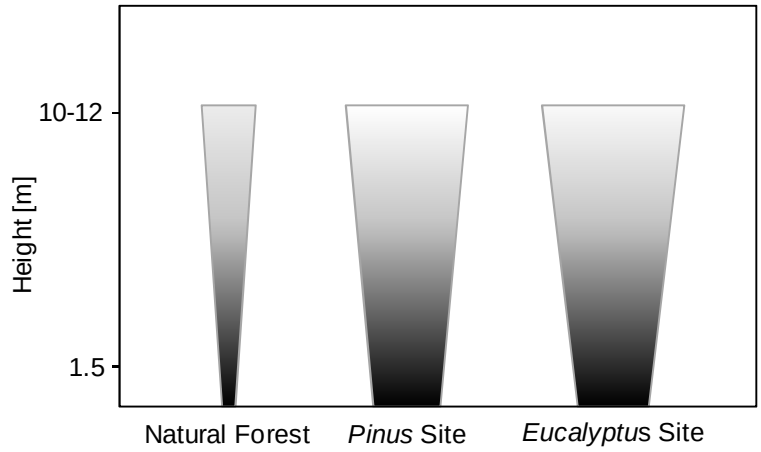

Figure 20: Visualization of gradients of monthly means of the daily sums of photosynthetic active radiation (PAR) between the understorey at saplings (at 1.5 m) and the sub-canopy levels (between 10 and 12 m above ground).

3.3.3 Daily courses of microclimate factors revealed by mean hourly values

Because monthly means equalize minima and maxima, and thus do not show differences in the actual values during the day, diurnal courses of selected typical days in the rainy and dry season shall be compared in the following section for a more detailed differentiation between sub-canopy spaces in the natural forest and the plantations. Because only 2 microclimate stations were available in addition to the reference station and one of them was maintained in the natural forest, data from the same days could not be recorded simultaneously in the two plantations.

3.3.3.1 Diurnal course of air temperature and VPD– examples for dry and rainy season days at the saplings level

In the course of a day, air temperature in the plantations was only slightly higher compared to the natural forest (Figure 21). Daily fluctuations of air temperature were less obvious in the rainy season in all sites with values ranging between 13 ℃ in the early morning and 20 ℃ in the afternoon (Figure 21 A and B). Temperatures above 15 ℃ lasted between 6 and 8 hours, maxima occurred between 14:00 and 16:00 h. In the dry season, the daily variations were higher. Around sunrise temperatures dropped to 7 ℃ but rose up to 24 ℃ around noon. (Figure 21 C and D). Daily maxima were recorded

between 15:00 and 16:00 h. Decrease of air temperatures after sunset was delayed by a few hours as compared to the situation during the rainy season.

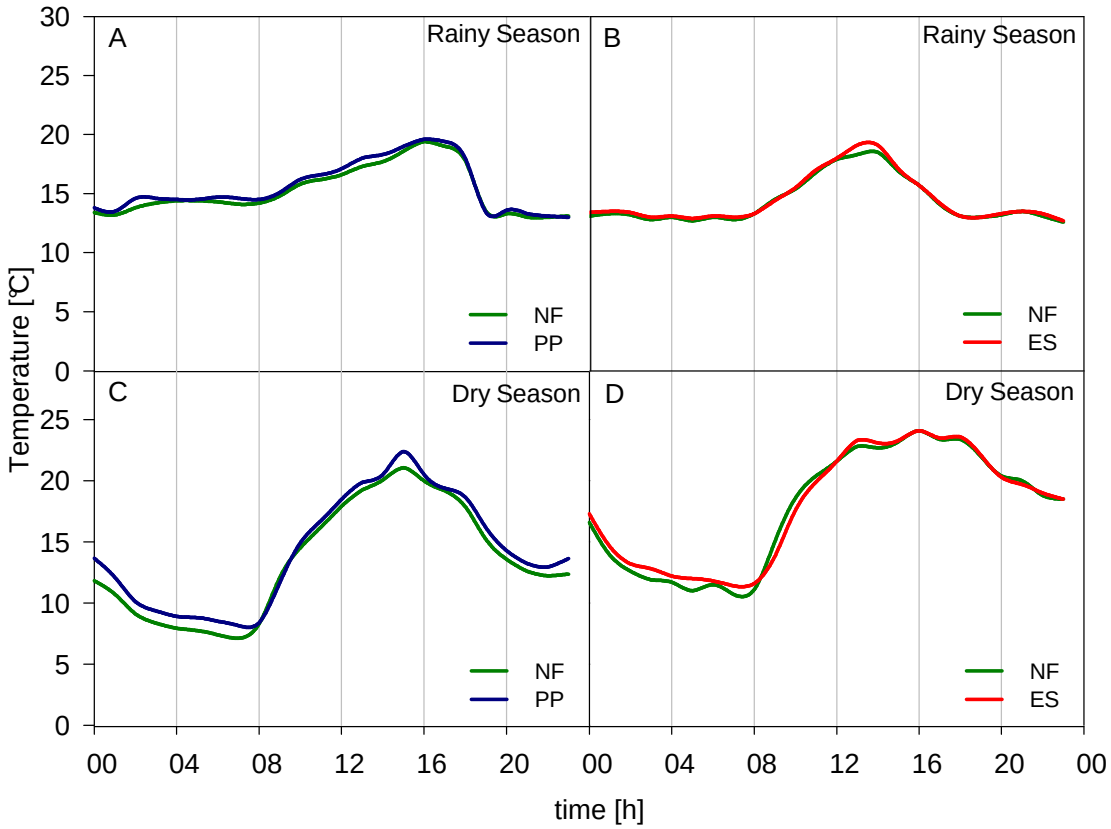

Figure 21: Daily courses of hourly means of air temperature in the three forest types at saplings level. A: In the natural forest and in the *Pinus* plantation on a rainy day (July 3, 2006). B: In the natural forest and in the *Eucalyptus* plantation on a rainy day (June 2, 2006). C: In the natural forest and in the *Pinus* plantation on a sunny day (November 8, 2005). D: In the natural forest and in the *Eucalyptus* plantation on a sunny day (March 8, 2006).

The daily course of VPD followed in general that of the air temperature suggesting that the total amount of water vapour in the air did not change very much in the course of the day. VPD increased in the morning, attaining its maximum between noon and 16:00 h and subsequently decreased reaching its minimum around 8:00 h, or as in the rainy season already shortly after sunset. While VPD approached zero during a rainy season night, it stayed rather high in the dry season. This is not unexpected but worth mentioning with regard to the stomatal behaviour described under 3.4.4 (Correlation between PAR, CO_2 net uptake and stomatal conductance). On rainy days VPD fluctuated in a small range between 0 and 1.2 hPa, while daily fluctuations on sunny days were about three times as much between 0.3 and 3.7 hPa. On a dry season day VPD in the *Pinus* plantation was up to 0.7 hPa higher than under the canopy of the

natural forest while on rainy days the difference was only 0.2 hPa. (Figure 22 A & C). Under the canopy of *Eucalyptus* (Figure 22 B & D) VPD was only for a few hours in the afternoon higher than that in the natural forest, and the differences between the *Eucalyptus* plantation and the natural forest on the whole were smaller. Nevertheless, in general VPD was higher in the plantations than in the natural forest (Figure 22).

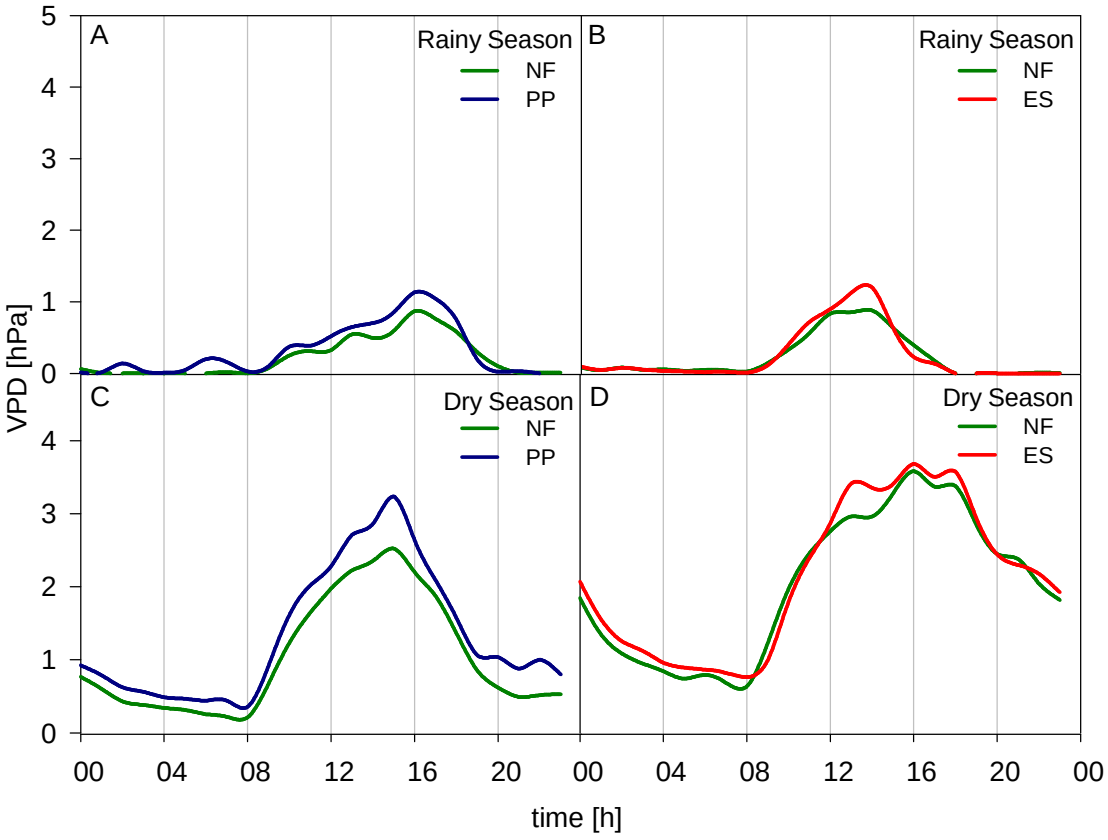

Figure 22: Daily courses of mean hourly VPD in the three forests at saplings level. A: In the natural forest and in the *Pinus* plantation on a rainy day (July 3, 2006). B: In the natural forest and in the *Eucalyptus* plantation on a rainy day (June 2, 2006). C: In the natural forest and in the *Pinus* plantation on a sunny day (November 8, 2005). D: In the natural forest and in the *Eucalyptus* plantation on a sunny day (March 8, 2006).

3.3.3.2 Daily course of PAR at saplings level – examples for dry and rainy season days

Photosynthetic active radiation (PAR) was considerably higher in the plantations compared to the natural forest (Figure 23). Under the canopy of *Pinus* maximum daily flux rates of PAR were up to 9 times higher on a rainy day and up to 8 times higher in the dry season, respectively (Figure 23 A and C). Under *Eucalyptus*, the corresponding rates of PAR were up to 5 times higher on a rainy, and up to 6 times higher on a day in the dry season (Figure 23 B and D). Maximum midday values of PAR were similar in

both plantations on rainy days with 43 and 47 µmol m^{-2} s^{-1} in the *Pinus* and the *Eucalyptus* plantation, respectively (Figure 23 A and B). In the dry season, highest midday values were about twice as high (under *Pinus* 105, under *Eucalyptus* 80 µmol m^{-2} s^{-1} (Figure 23 C & D). The highest midday values in the natural forest were only between 5 and 10 µmol m^{-2} s^{-1} on rainy (Figure 23 A & B) and about 13 and 14 µmol m^{-2} s^{-1} (Figure 23 C and D) on sunny days.

The daily courses of PAR show a simultaneous start in the morning around 7:00 h for the *Eucalyptus* plantation and the natural forest, whereas, due to the more open canopy of the *Pinus* plantation, PAR rose one hour earlier in both season (Figure 23 A and C).

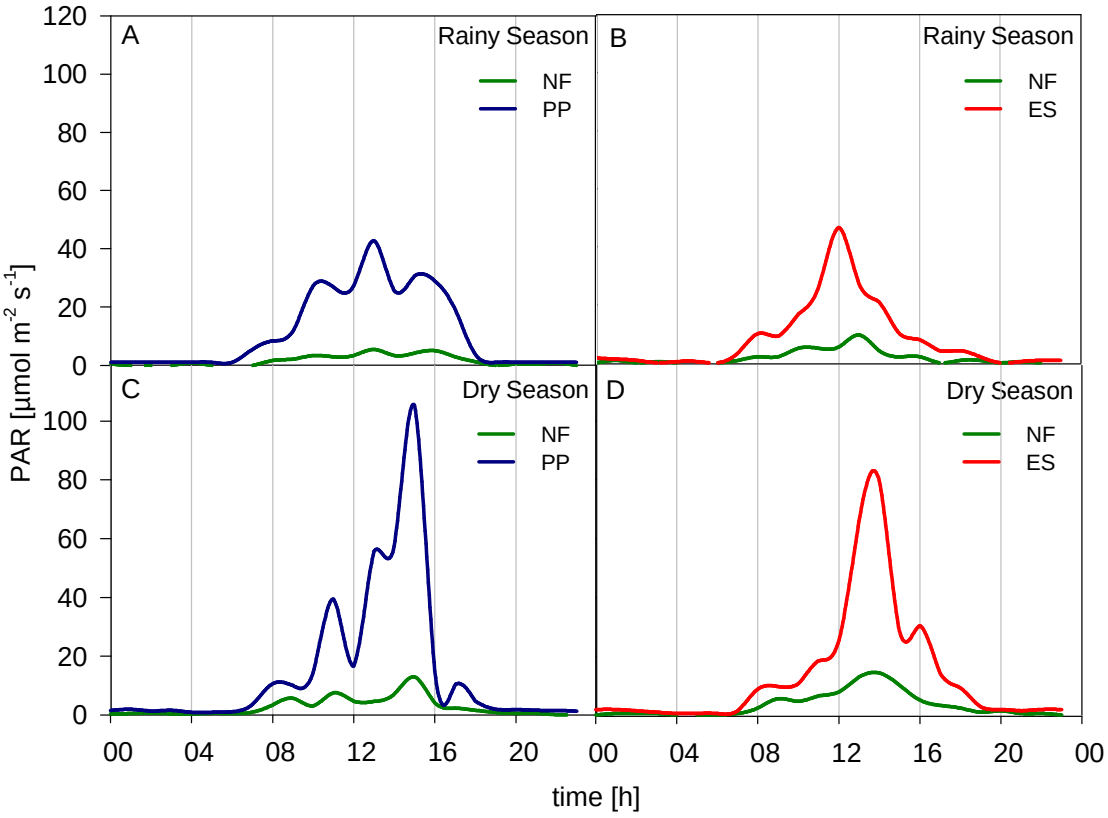

Figure 23: Daily courses of mean hourly photosynthetic active radiation (PAR) in the three forest types at saplings level. A: In the natural forest and in the *Pinus* plantation on a rainy day (July 3, 2006). B: In the natural forest and in the *Eucalyptus* plantation on a rainy day (June 2, 2006). C: In the natural forest and in the *Pinus* plantation on a sunny day (November 8, 2005). D: In the natural forest and in the *Eucalyptus* plantation on a sunny day (March 8, 2006).

3.3.4 Daily averages and sums, respectively, of the variables of the understorey microclimates

A summary of the daily courses of the microclimate variables of the understorey space, as presented in Figure 21 to Figure 23 for the example days, is shown in Table 4. Daily sums are given for PAR and throughfall, mean values for air temperature and VPD.

PAR at the saplings' level was consistently higher in the plantations than in the natural forest, irrespective of the season. On the example days given in Table 4, PAR in the natural forest was on average 16% of that in the *Pinus* plantation and 23% of that in the *Eucalyptus* plantation.

Differences of the daily average in air temperature and vapour pressure deficit between the sites were negligible in the rainy season and only slightly more apparent in the dry season. In the *Pinus* plantation at saplings level, daily mean temperature was 0.8 ℃ and averaged VPD was 0.2 hPa higher than in the natural forest. Under *Eucalyptus*, averaged daily temperature and VPD did not differ substantially from those under the natural canopy.

The daily sums of the throughfall showed comparable values for the natural forest and the *Pinus* plantation, whereas in the *Eucalyptus* plantation, 40% of the throughfall, compared to the sums in the natural forest, were already taken away by evaporation and interception in the plantations.

Table 4: Characterization of the sub-canopy microclimates of the three forest types. Daily averages (temperature, VPD) and sums (PAR, throughfall) of the microclimate in the natural forest (NF) and the plantations (PP and ES) on selected days in the dry and rainy season

	Rainy season (July 3, 2006)		Rainy season (June 2, 2006)		Dry season (Nov 8, 2005)		Dry season (March 8, 2006)	
	NF	**PP**	**NF**	**ES**	**NF**	**PP**	**NF**	**ES**
PAR [mol m^{-2} d^{-1}]	0.14	1.02	0.15	0.71	0.23	1.29	0.29	1.15
Temperature [℃]	15.2	15.5	14.3	14.5	13.4	14.2	17.7	17.9
VPD [hPa]	0.20	0.30	0.22	0.24	1.06	1.28	2.01	2.12
Throughfall [mm d^{-1}]	9.7	9.2	11.3	6.8				

3.4 Photosynthesis

3.4.1 Investigation of factors influencing CO_2 net uptake

3.4.1.1 Influence of climate factors

To assess the importance of the different environmental factors on photosynthetic carbon gain, CO_2 net uptake of a *Podocarpus* sapling was measured at four different light levels (100, 500, 1000 and 1500 µmol m^{-2} s^{-1}), under dry season conditions with air temperature ranging from 14.5 to 32 °C and relative humidity ranging from 22 to 66% and a VPD between 0.2 and 3.9 hPa (Figure 24).

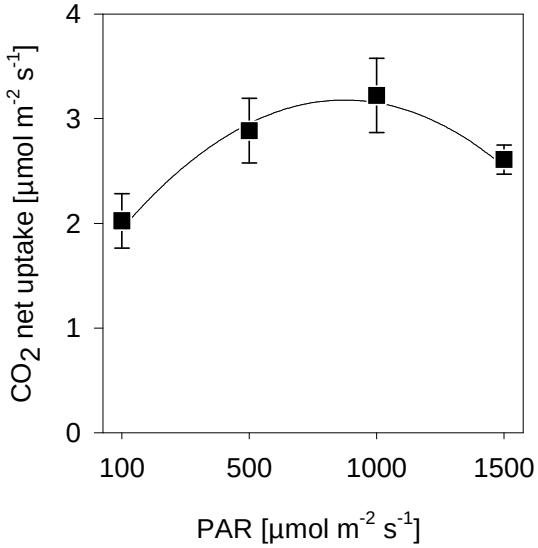

Figure 24: Correlation between different PAR intensities and CO_2 net uptake under ambient conditions, i.e. varying temperature and relative humidity. Each data point shows the mean value (± SE) of CO_2 net uptake when rel. humidity changed between 22 and 66%, and the temperature between 15 and 32 °C. The quadratic model graph is based on the parameter estimates of the quadratic model given in Table 5

Significant effects were found for PAR ($F_{1,154}$ = 375.39; p < 0.001) and air temperature ($F_{1,154}$ = 19.04; p < 0.001), but not for relative humidity (Table 5). The effect of PAR, which results in an optimum for CO_2 net uptake between 500 and 1000 µmol m^{-2} s^{-1} (Table 5), explained 71% (r^2 = 0.712) of the variations of CO_2 net uptake.

When relative humidity and air temperature were replaced by VPD, the significant levels showed similar results. Both, PAR ($F_{1,154}$ = 321.51; p < 0.001) and VPD ($F_{1,154}$ = 14.53; p < 0.001), were significantly influencing CO_2 net uptake. Both climate factors together explained 75% (r^2 = 0.753) of the variations of the net CO_2 uptake, with a proportion of

PAR of 71% and of VPD of 4%. There were no significant interactions between the factors.

Table 5: Examination of the significance of microclimate effects on photosynthetic CO_2 net uptake by leaves of *Podocarpus falcatus* saplings by the quadratic model applied to four levels of PAR and the ranges of varying rH, VPD and temperature described above.

	DF	F-value	p-value
PAR	1,154	375.39	**< 0.001**
(PAR)²	1,154	243.45	**< 0.001**
Rel. humidity	1,154	0.22	0.64
Temperature	1,154	19.04	**< 0.001**
VPD	1,154	14.53	**< 0.001**

3.4.1.2 Light saturation

Light response curves of CO_2 net uptake at ambient CO_2 concentration, constant temperature and relative humidity were similar with leaves from the *Podocarpus* saplings under all three canopy types (Figure 25 A to C), but the rates measured with saplings growing outside the shelter in the open area were by 20% lower (Figure 25 D) at low light intensities. A linear increase was observed up to 100 µmol PAR m^{-2} s^{-1} and light saturation was achieved between 1500 and 2000 µmol m^{-2} s^{-1}. Maximal rates of CO_2 net uptake were between 2.4 (leaves from saplings in the open site) and 2.9 µmol m^{-2} s^{-1} (leaves of saplings in the *Pinus* site).

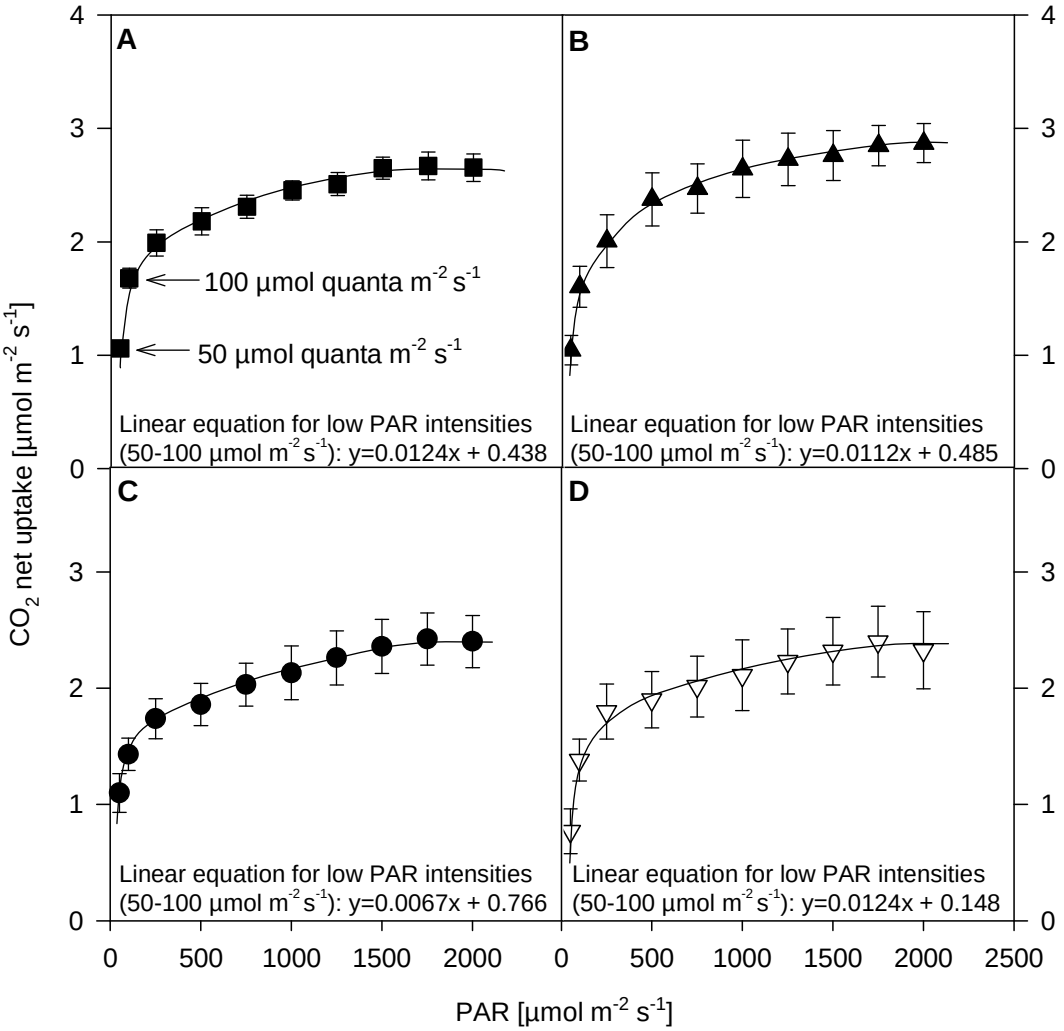

Figure 25: Light (PAR) response curves of photosynthetic CO_2 net uptake by leaves of *Podocarpus* saplings growing under the canopies of the natural forest (A), of *Pinus patula* (B), *Eucalyptus saligna* (C) and without shelter in an open site (D). Data show mean values of two to five saplings per site with 3 repetitions per leaf (± S.E.)

3.4.1.3 Experimental simulation of the influence of sunflecks on photosynthetic net CO_2 uptake

The light climate under the canopy of shelter-trees consists of diffuse and direct radiation (sunflecks). The effect of the varying sub-canopy light intensities on photosynthesis of the young *Podocarpus* trees was examined by simulating sunflecks with the artificial PAR source of the porometer at otherwise ambient conditions (Figure 26 B) and comparing it with the effect of a continuous illumination with the same amount of quanta and over the same time period (Figure 26 A). Net CO_2 uptake rates were investigated under different light conditions (82, 40, 200 and 400 µmol m^{-2} s^{-1},

respectively), but at constant relative humidity (60%) and temperature (20 ℃). Pre-illuminated leaves were used for that experiment. Net CO_2 uptake rates under the constant light level of 82 µmol m^{-2} s^{-1} were slightly above 2 µmol m^{-2} s^{-1}, whereas under changing light conditions of 30 µmol m^{-2} s^{-1} as the basic light intensity and lightflecks of 200 and 400 µmol m^{-2} s^{-1}, respectively, net CO_2 uptake rates varied between 0.8 and 2.2 µmol m^{-2} s^{-1}. Photosynthetic CO_2 uptake responded with a delay of 8-10 seconds to the increase of the light intensity and returned to the low-light level about 40 seconds after termination of the lightfleck (Figure 26 B). Comparing the photosynthetic carbon gain in both experimental variants, in which the same amount of PAR was administered over the same time period shows that the variant with lightflecks was less effective than the continuous illumination (mean CO_2 net uptake under changing light conditions 1.52 µmol m^{-2} s^{-1} and 2.07 µmol m^{-2} s^{-1} under constant illumination). CO_2 net uptake triggered by 400 µmol PAR m^{-2} s^{-1} lightflecks was only 1.18 times higher than that resulting from a lightfleck of 200 µmol m^{-2} s^{-1}. While the applied PAR intensities of the continuous illumination (82 µmol m^{-2} s^{-1} Figure 26 A) and the basic radiation in the lightfleck experiment (40 µmol m^{-2} s^{-1}) were within the linear range of the light response, the lightfleck intensity (200 µmol m^{-2} s^{-1}) extended into the non-linear range.

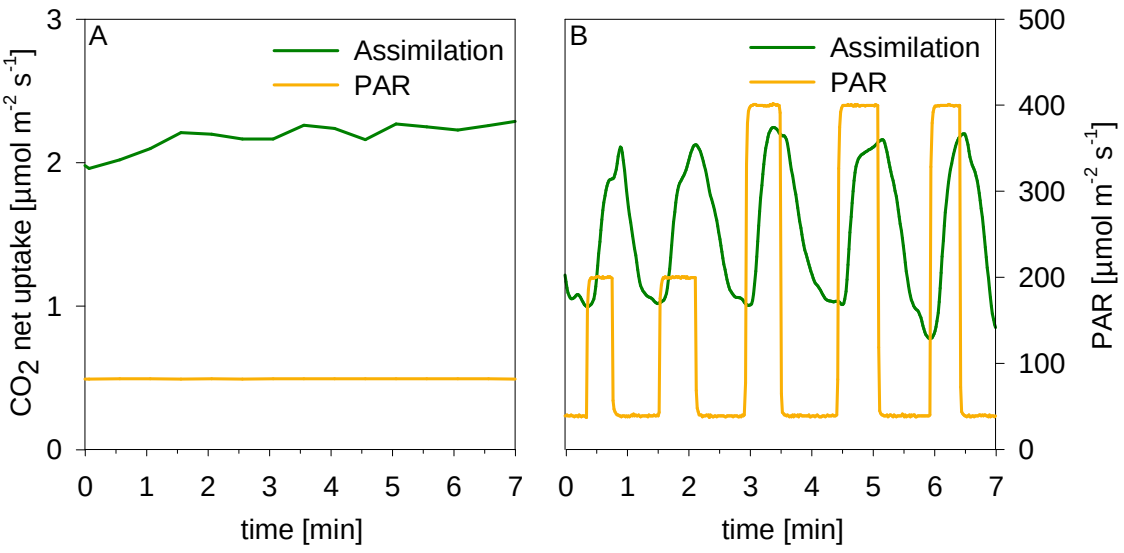

Figure 26: Analysis of the lightfleck effect on photosynthetic CO_2 uptake by two artificial light conditions, providing the same amounts of PAR over an identical time-span. PAR provided as constant photon flux density of 83 µmol m^{-2} s^{-1} (A), PAR provided as intermittent lightflecks of 30 s at an intensity of 200 or 400 µmol m^{-2} s^{-1} superimposed on a basic intensity of 40 µmol m^{-2} s^{-1} (B). The interval between the individual lightflecks was 60 s.

3.4.2 Sunflecks

3.4.2.1 Effect of the number and frequency of sunflecks on the daily net CO_2 uptake

Taking the results of the experiment on the effect of lightflecks on photosynthetic CO_2 uptake (Figure 26) as a basis, an attempt was made to characterize the sub-canopy light climates of the 3 sites in a synopsis of light intensities and their temporal distribution over the day. The light intensities were categorized with respect to their photosynthetic efficiencies derived from the light response curves. The following light intensity classes (in µmol m^{-2} s^{-1}) were differentiated: 0 - 40 (diffuse light, shade), 40 - 70 (small sunflecks), 70 - 100 (sunflecks of intensities reaching the upper end of the linear light response), 100 - 500 (sunflecks in the curvilinear range of the light response curve), 500 - 1000 (sunflecks reaching light saturation of photosynthesis) and > 1000 (lightflecks exceeding light saturation). Partitioning of the linear phase of the photosynthetic light response curve was necessary because of the temporal intervals of 1 min which were used in the examination of the daily courses. Both the light (PAR) intensity classes and their duration were related to the total daily accumulated irradiation and the duration of the daily light period. For comparison of the light climates all complete daily courses of environmental data (and also photosynthetic CO_2 uptake) were used, irrespective of having been taken during the dry or the rainy season. The results shown in Figure 27 A and B reveal considerable differences of the sub-canopy light climates of the three sites. The greatest share of the lowest light intensity in the total accumulated PAR and at the same time the greatest share in the daily light period was observed in the *Eucalyptus* plantation. Likewise, the portion of the low intensity sunflecks (11%) and their duration (12%) was lowest in that site. The share of the most effective sunflecks up to 100 µmol m^{-2} s^{-1} was 6%, but summed up to only 5% of the daily light period. The proportion of the sunflecks in the curvilinear range of the light response curve and up to light saturation was about 21%, but composed of very short events amounting to not more than about 10% of the photosynthetically active light period. Sunflecks exceeding light saturation of photosynthesis were hardly observed. With respect to photosynthesis the light climate under the canopy of *Pinus* was much better: Diffuse PAR had a share of less than 30% in the accumulated irradiation and the lowest temporal share of the 3 sites. On the other hand the most effective sunflecks had the greatest shares of both the accumulated PAR and the time. This holds also for the sunflecks in the curvilinear range of the light response curve and the shares up to light saturation. But there is also a high proportion

(about 8%) of lightflecks exceeding light saturation which decrease the overall photosynthetic efficiency of the light climate. Expectedly the share of such sunflecks in the daily light period was, however, small (about 2%). The light climate under the natural canopy when considered all together was in both respects, the shares of light intensity classes and their temporal contribution, in between the *Eucalyptus* and the *Pinus* sites. Despite the high degree of canopy closure (Table 2) almost as many high intensity sunflecks (PAR) reached the *Podocarpus* saplings in the natural forests as under the patchy *Pinus* shelter. But the time period associated with these sunflecks was shorter than under *Pinus*.

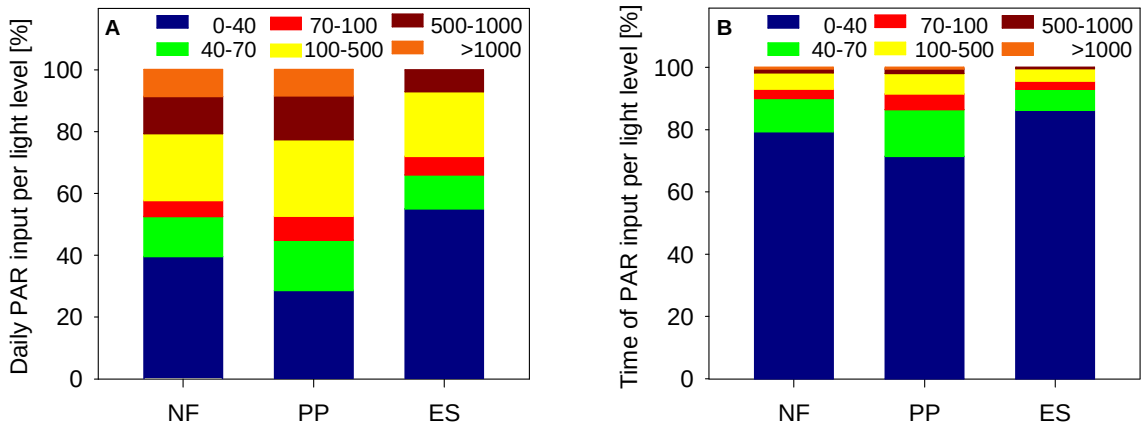

Figure 27: Percentage of daily PAR (A) at the saplings' level, and (B) time spans (relative to the daily light period) of PAR input at the different sites, separated into different light intensities of 0 - 40 (diffuse light, blue), 40-70 (green), 70 - 100 (red), 100 - 500 (yellow), 500 - 1000 (dark red) and > 1000 (orange) µmol m^{-2} s^{-1}.

3.4.2.2 Classification of the three sub-canopy light climates by light intensity and temporal shares of light intensity classes

Figure 28 shows three daily courses of CO_2 net uptake (A), PAR, temperature, stomatal conductance (g_s) and transpiration (E) which are considered typical of the selected weather situations and forest types. Panels a to d represent dry weather conditions in the natural forest and the *Pinus* plantation, respectively, and panels e and f show the situation on an overcast day in the *Eucalyptus* plantation with some drizzle in the afternoon at the beginning of the rainy season. At the early dry season (panels a - d) the soils were still moist and thus water supply to the trees was sufficient resulting in a generally high stomatal conductance. By contrast, soils were still rather dry at the

beginning of the rainy season and water supply may have run short especially during the afternoons resulting in a lower stomatal conductance.

Given sufficient stomatal conductance (g_s >10 mmol m^{-2} s^{-1} and E up to 1.5 mmol m^{-2} s^{-1}), photosynthetic CO_2 net uptake responded very sensitive to any change in the light intensity, especially during the morning hours. In the afternoon, when stomatal conductance was low, sunflecks resulted only in small responses of CO_2 net uptake (e.g. Figure 28 panels a and b after 15:00 h and Figure 28 e and f between 15:00 and 16:00 h). The limiting effect of the stomatal conductance on net carbon uptake is also obvious from panels c and d. As long as stomatal conductance was high, transpiration increased during the morning hours (Figure 28 b, d, f) whereas it followed closely stomatal conductance in the course of the afternoon when the relative humidity of the air was low.

Although the average numbers of sunflecks were in a similar range of 30 to 40 per day in all 3 forest types (Table 7) and not necessarily higher on sunny than on cloudy days, the average daily sums of PAR are consistently higher on sunny days. Due to differences in the structure and density of the canopies, the duration and intensities of the sunflecks and thus their contributions to the daily accumulated PAR were different. Long lasting sunflecks of high intensity were recorded under the *Pinus* canopy (see also Figure 28 c) and to some extent also under the shelter of the natural forest (Figure 28 a). Therefore the contributions to the total daily PAR sums were rather high (55 - 72%), whereas the share of the shorter and less intense sunflecks under the *Eucalyptus* canopy was significantly smaller (40 - 51%) and conversely, the contribution of the diffuse radiation was significantly higher. The differences in the photosynthetic efficiencies of the three sub-canopy light climates become understandable on the background of the results of the experiment with artificial lightflecks (Figure 26). Only around 30% of the daily CO_2 uptake by the *Podocarpus* saplings in the *Eucalyptus* plantation resulted from sunflecks and 70% from the more effective low energy diffusive radiation, whereas considerably higher shares of sunfleck-driven and with regard to yield less effective photosynthesis were recorded in the natural forest and in particular in the *Pinus* plantation.

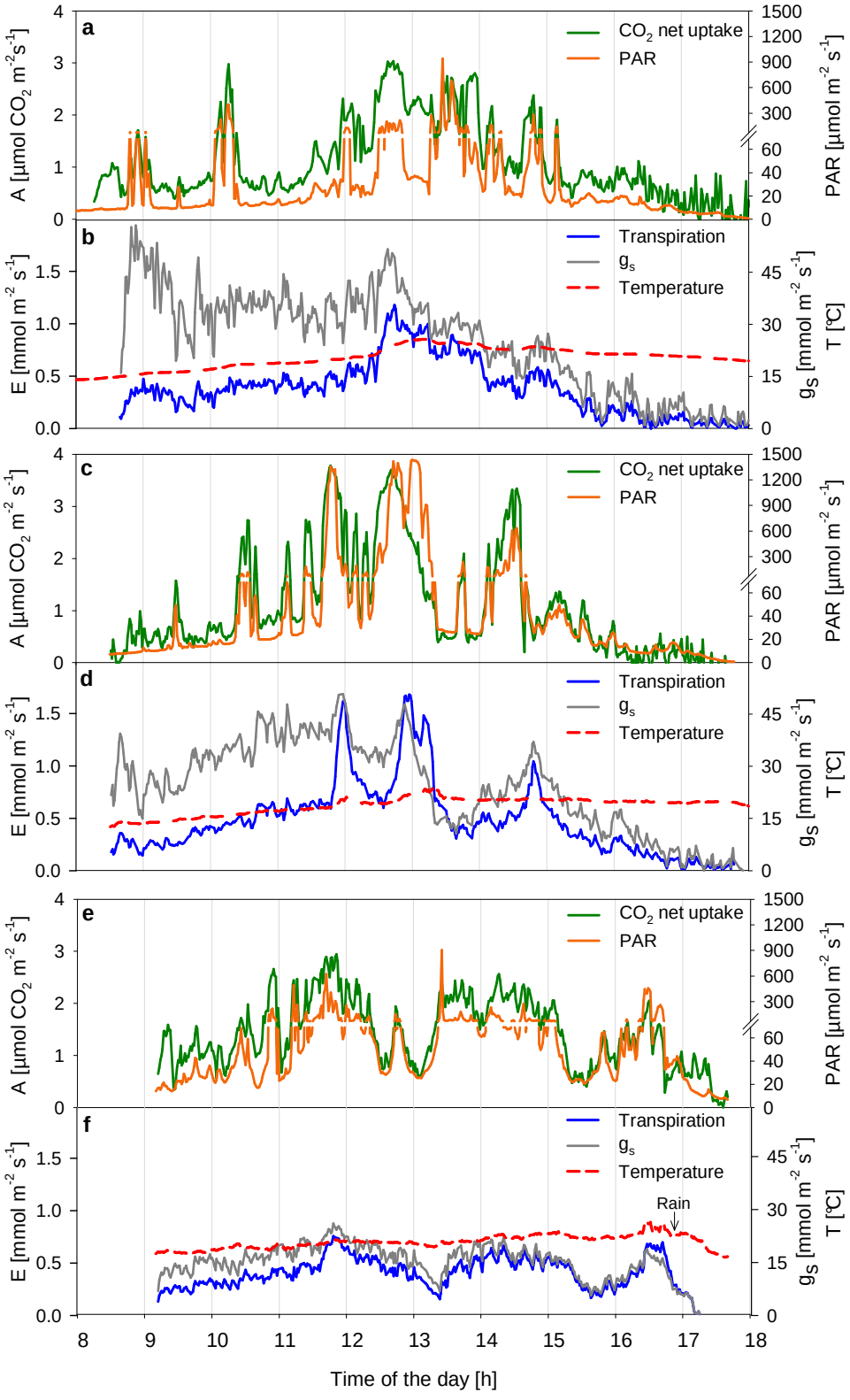

Figure 28: Daily courses of CO_2 net uptake (A), of stomatal conductance (g_s) and transpiration (E) by *Podocarpus* saplings, and of PAR and air temperature on a sunny day (24. Nov. 2006) in the natural forest (a, b); on a sunny day (12. Dec. 2006) in the *Pinus* plantation (c, d); and on a cloudy day with some drizzle (20. March 2006) in the *Eucalyptus* plantation (e, f). Total sums of CO_2 net uptake: 36.4 (a), 34.7 (c) and 48.0 (e) mmol m^{-2} d^{-1}; total sums of PAR: 1.5 (a), 4.7 (c) and 2.5 (e) mol m^{-2} d^{-1}.

3.4.2.3 The role of sunflecks in the daily CO_2 uptake

Table 6 shows the differences between a light climate with sunflecks and a virtual, equally distributed constant light intensity. The daily accumulated PAR and the daily carbon uptake measured in the different sites under cloudy and clear sky are compared with an estimated daily carbon gain, calculated from the average PAR intensity during the day and the corresponding CO_2 net uptake calculated from the light response curves (Figure 25). The efficiency is calculated as percentage of the measured from the estimated CO_2 net uptake. The highest efficiency, near 100%, was reached in the *Pinus* plantation on cloudy days while on sunny days with higher PAR input, the efficiency was less reaching only 70%. In the natural forest, the apparent efficiency did not differ considerably between cloudy and sunny days, but as under *Pinus* it was higher under cloudy conditions (86% and 80% for cloudy and sunny days, respectively). Efficiency of the actual PAR under the canopy of *Eucalyptus* was also higher on cloudy days, but in general the efficiencies were much lower with 72% and 53% for cloudy and sunny days, respectively.

Table 6: Photosynthetic efficiency of the actual sub-canopy light climate compared to a virtual constant illumination with the same amounts of PAR applied over the same time period. Estimated daily CO_2 net uptake was calculated using the light response curves of CO_2 net uptake shown in Figure 25.

Forest/ plantation	Climate condition	Daily sum of PAR [mol m^{-2} d^{-1}]	Average PAR intensity [µmol m^{-2} s^{-1}]	Estimated daily CO_2 net uptake [mmol m^{-2} d^{-1}]	Measured daily CO_2 net uptake [mmol m^{-2} d^{-1}]	Apparent efficiency of the actual radiation [%]
Natural	cloudy	1.40	40.3	32.1	27.5	86
forest	sunny	1.63	48.0	35.3	28.3	80
Pinus	cloudy	1.56	45.7	34.1	33.0	97
plantation	sunny	2.04	59.8	39.5	27.8	70
Eucalyptus	cloudy	0.92	27.0	32.4	23.4	72
plantation	sunny	1.08	31.5	33.4	17.6	53

3.4.3 Daily accumulated PAR and carbon gain

Daily amounts of PAR reaching the individual differed between cloudy and sunny days and from site to site (Table 7). In the natural forest the daily amounts of PAR varied from 450 to 2840 mmol m^{-2} d^{-1} with a mean value (n = 8) of 1400 mmol m^{-2} d^{-1} for rainy conditions and 1630 mmol m^{-2} d^{-1} for sunny days (n = 8). In the *Pinus* plantation, the span of the daily PAR sums was wider with corresponding values between 430 and

4730 mmol m^{-2} d^{-1} and averages of 1560 and 2050 mmol m^{-2} d^{-1} under cloudy (*n* = 9) and sunny weather conditions (*n* = 13), respectively. In the *Eucalyptus* site the spans of the daily amounts of PAR were comparable to those of the natural forest ranging from 240 to 2680 mmol m^{-2} d^{-1}. However, the mean values were considerably lower than in the natural forest with 920 mmol m^{-2} d^{-1} under cloudy sky (*n* = 8) and 1080 mmol m^{-2} d^{-1} under sunny conditions (*n* = 13).

The number of daily sunflecks did not differ very much on the three sites with average values between 31 and 40. Depending on the weather condition, i.e. cloudiness, the number as such could be even higher on a cloudy than on a sunny day (*Pinus* site). The duration of the individual sunflecks was similarly depending on the cloud cover and usually longer sunflecks were observed on sunny days.

The percentage of daily accumulated PAR resulting from sunflecks was highest in the *Pinus* plantation irrespective of the weather conditions (71% and 72% on cloudy and sunny days, respectively). In the *Eucalyptus* site, sunflecks accounted for 40% of the daily PAR under cloudy sky and 51% on sunny days. In the natural forest, the share of PAR resulting from sunflecks was slightly higher with 55% and 67% under cloudy and sunny weather condition, respectively.

The values of all photosynthetic measurements of *Podocarpus* saplings showed a significantly lower carbon gain of the saplings in the *Eucalyptus* plantation compared to saplings in the natural forest (*p* = 0.04) and the *Pinus* site (*p* = 0.003) (Table 6), whereas the difference between carbon uptake by the saplings in the natural forest and the *Pinus* plantation was statistically not significant. Likewise, the mean values did not differ significantly between cloudy and sunny days. In the *Eucalyptus* site, the daily carbon gains of the *Podocarpus* saplings ranged between 4 to 38 mmol m^{-2} d^{-1}, and the daily averages differed under cloudy (23 mmol m^{-2} d^{-1}) and sunny weather (18 mmol m^{-2} d^{-1}).

In accordance with the daily share of sunflecks in accumulated PAR, the percentage of the daily CO_2 uptake resulting from sunflecks was lowest under *Eucalyptus* and more CO_2 was assimilated on sunny than on rainy days. In contrast, in spite of the higher share of sunflecks of the total PAR, CO_2 uptake resulting from sunflecks was higher under cloudy sky than on sunny days in the other two forest sites. As could be expected from the high contribution of sunflecks to the daily PAR, CO_2 uptake by the *Podocarpus* saplings, attributable to sunflecks, was highest in the *Pinus* plantation.

Table 7: The sub-canopy light climates of the 3 investigated forest areas and their effects on photosynthetic CO_2 net uptake. With regard to the typical weather situations 2 classes of the daily accumulated global radiation were defined: 19 - 59 mol m^{-2} d^{-1} for cloudy days with drizzle, typical for the wet season and 60 - 82 mol m^{-2} d^{-1} for sunny days of the dry season. Means ± S.E., different lowercase letters indicate differences between the sites.

	Natural forest		*Pinus* plantation		*Eucalyptus* plantation	
Number of analyzed daily courses	8	8	9	13	8	13
Weather condition	cloudy	sunny	cloudy	sunny	cloudy	sunny
Daily accumulated PAR [mmol m^{-2} d^{-1}]	**1399^{ab}** ± 306	**1630^{ab}** ± 309	**1563^{ab}** ± 185	**2044^{a}** ± 322	**924^{b}** ± 248	**1080^{b}** ± 195
Daily numbers of sunflecks > 40 µmol m^{-2} s^{-1}	31^{a} ± 4	39^{a} ± 4	40^{a} ± 2	33^{a} ± 3	35^{a} ± 5	35^{a} ± 4
Percent of daily accumulated PAR resulting from sunflecks > 40 µmol m^{-2} s^{-1}	55	67	71	72	40	51
Daily CO_2 net uptake [mmol m^{-2} d^{-1}]	**28^{a}** ± 3	**27^{a}** ± 4	**33^{a}** ± 3	**28^{a}** ± 2	**23^{ab}** ± 4	**18^{b}** ± 3
Percent of daily CO2 net uptake resulting from sunflecks > 40 µmol m^{-2} s^{-1}	41	38	62	48	27	31

3.4.4 Correlation between PAR, CO_2 net uptake and stomatal conductance

Table 8 shows the correlations between PAR and CO_2 net uptake, between stomatal conductance and CO_2 net uptake and between PAR and stomatal conductance. The relationship between PAR and assimilation did not differ much between the sites. In general, the relationship was slightly better before noon (r^2 = 0.57 to 0.65) compared to the afternoon values (r^2 = 0.46 to 0.52) when stomatal conductance comes into play.

The correlation between stomatal conductance and CO_2 net uptake differs between the sites. The strongest correlation is found in the natural forest, where 46% of the assimilation could be explained by stomatal conductance. Also in the *Eucalyptus* site, the relation between the two parameters is still strong with r^2 = 0.38, whereas in the *Pinus* plantation, the relation between the two parameters is not that obvious (r^2 = 0.29). In all sites, the correlation is considerably stronger in the afternoon compared to the

morning hours. The correlation between PAR and stomatal conductance is ambiguous. The best relation is found in the *Pinus* plantation ($r^2 = 0.28$), here the difference between morning and afternoon values is only small. In the natural forest the correlation is weak the afternoon ($r^2 = 0.29$), whereas in the morning, no correlation was observed. In the *Eucalyptus* plantation, the correlation was very weak during the whole day ($r^2 = 0.13$).

Table 8: Correlation between photosynthetic active radiation and CO_2 net uptake (PAR/A), between stomatal conductance and CO_2 net uptake (g_s/A), and between photosynthetic active radiation and stomatal conductance (PAR/g_s) of the saplings in the three different sites. Numbers given are correlation factors (r^2) between the datasets of 17, 22 and 18 daily courses in the natural forest, the *Pinus* and the *Eucalyptus* plantation, respectively, on the one hand (bold), and the three daily courses shown in Figure 28 on the other.

	n	PAR/A [r^2]	g_s/A [r^2]	PAR/g_s [r^2]
Natural forest				
whole day	**17**	**0.53**	**0.46**	**0.19**
morning (8:30-13:00)	**17**	**0.57**	**0.24**	**0.10**
afternoon(13:00-18.00)	**17**	**0.49**	**0.66**	**0.29**
Figure 28 b morning	1	**0.75**	**0.24**	**0.18**
Figure 28 b afternoon	1	**0.56**	**0.83**	**0.44**
***Pinus* plantation**				
whole day	**22**	**0.56**	**0.29**	**0.28**
morning (8:30-13:00)	**22**	**0.61**	**0.33**	**0.27**
afternoon(13:00-18.00)	**22**	**0.52**	**0.58**	**0.33**
Figure 28 d morning	1	0.78	0.46	0.16
Figure 28 d afternoon	1	0.57	0.76	0.60
***Eucalyptus* plantation**				
whole day	**18**	**0.56**	**0.38**	**0.13**
morning (8:30-13:00)	**18**	**0.65**	**0.22**	**0.12**
afternoon(13:00-18.00)	**18**	**0.46**	**0.51**	**0.15**
Figure 28 f morning	1	0.75	0.66	0.56
Figure 28 f afternoon	1	0.50	0.67	0.32

3.5 CO_2 net uptake of the *Podocarpus falcatus* shelter-tree in comparison to the saplings

To show the difference between the young *Podocarpus* saplings and the mature tree, light saturation curves, the daily course of CO_2 net uptake and the daily sums of carbon gain investigated.

3.5.1 Light response curve

The light response curve of leaves of a *Podocarpus* shelter-tree (Figure 29) is very similar to those of the saplings in the different sites, and the maximum rate is only slightly higher reaching 4.0 µmol m^{-2} s^{-1}. The linear section of the curve (at low PAR intensities) is very steep and saturation started at PAR values of 750 µmol m^{-2} s^{-1}, as with leaves of the saplings.

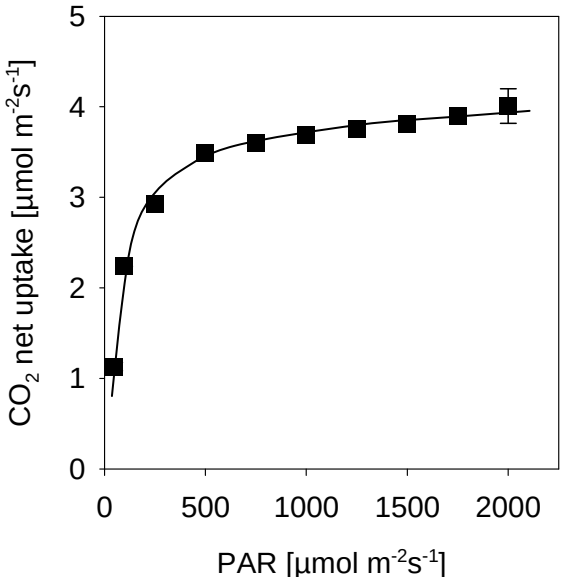

Figure 29: Photosynthetic light response curve of leaves of a *Podocarpus falcatus* shelter-tree in the natural forest. Data show mean values of five light response curves ± S.E.

3.5.2 Diurnal courses of net CO_2 uptake and PAR

CO_2 net uptake of the 17 m high *Podocarpus falcatus* shelter-tree was measured in the outer part of the sun crown (Figure 30) on a dry day in the rainy season on May 31 in 2006. PAR values above 400 µmol m^{-2} s^{-1} were already recorded in the morning around 9.00 h, followed by a continuous up and down until 14:45 h when the light intensity due to the inclination of the sun declined to a level below 200 µmol m^{-2} s^{-1}. CO_2 net uptake rates varied between 1.5 and 2.3 µmol m^{-2} s^{-1} at moderate and high light intensities, respectively, and between 0.8 and 1.6 µmol m^{-2} s^{-1} in the afternoon after 15:00 h.

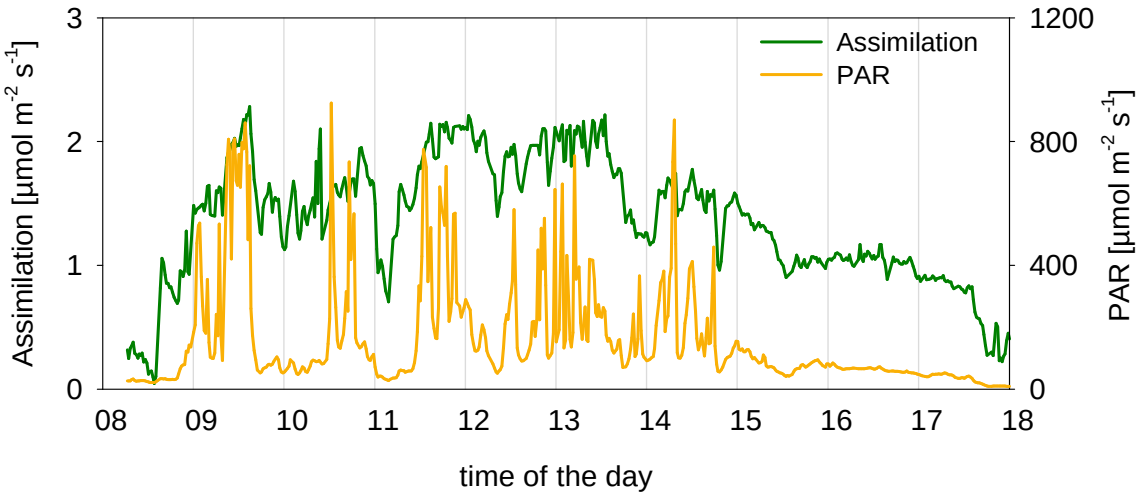

Figure 30: Diurnal course of net CO_2 uptake as related to PAR of leaves from of the sun-crown of the *Podocarpus falcatus* shelter-tree in the natural forest on a sunny day in the rainy season (May 31, 2006).

3.5.3 Carbon gain

Daily carbon gain of the *Podocarpus* shelter-tree was measured on 9 days in the sun crown at 12 m height under dry (n = 4) and cloudy (n = 5) weather conditions. Daily accumulated carbon gain was between 8.0 to 61.0 mmol m^{-2} d^{-1} with a mean value of 27.9 mmol m^{-2} d^{-1}. Respective daily PAR sums were between 0.3 and 4.4 mol m^{-2} d^{-1}, with a mean value of 1.9 mol m^{-2} d^{-1}.

3.6 Sap flow

Xylem sap flow was measured on young *Podocarpus falcatus* and on the shelter-trees. In addition to information about the water demand of the three tree species the question of a potential competition between the saplings and the adult shelter-trees was addressed. Unfortunately, the size of several of the *Podocarpus* saplings was too small for using the Granier method; in the natural forest the stems of the saplings were too thin for sap flow measurements. Therefore a bigger sapling with a dbh of 8.6 cm and a height of 7.6 m was selected. In the *Eucalyptus* site, a *Podocarpus falcatus* sapling of the same size (dbh 8.7 cm, 6.5 m) was used, whereas the *Podocarpus* sapling in the *Pinus* plantation was smaller (dbh 5.1 cm, height 4.8 m). Sap flow of the *Podocarpus* saplings and the shelter-trees was calculated from an equation derived from a calibration experiment (see methods section: Calibration of sap flow sensors). Sap flow

of *Pinus* and *Eucalyptus* was calculated from sap flow density and sap wood area, which could be determined from cross-section of felled trees. Sap wood area was on average 41% of the total stem area in *Pinus*, whereas in *Eucalyptus*, sap wood area decreased strongly with increasing tree diameter. Sap wood area of smaller trees was about 50 % of the stem area, in the big *Eucalyptus*, the sap wood area was only 26% of the stem area.

3.6.1 Diurnal courses of sap flow of the *Podocarpus falcatus* saplings as related to VPD under the different canopies

Diurnal courses of sap flow of the *Podocarpus* sapling in the natural forest are shown for two days of the rainy and the dry season (Figure 31). On a cloudy day in the rainy season (Figure 31 A), sap flow started late in the morning at 10:00 h and ceased in the evening around 21:30 h. During the day, the course followed in general VPD both showing a small depression during noon. Rates of sap flow were low reaching maximum values of 17.3 ml min^{-1}. The corresponding VPD was 7.0 hPa. During night time, sap flow was negligible, whereas VPD decreased slowly attaining its minimum in the morning at 8:00 h.

On a sunny day in the dry season (Figure 31 B), sap flow started already at 9:00 h and continued, finally at a low rate, until midnight. High values above 35 ml min^{-1} were recorded at noon between 11:30 and 15:00 h whereas VPD still increased and reached its maximum of 14.6 hPa later in the afternoon at 16:00 h. Like in the rainy season, VPD decreased slowly during the night, the lowest values were recorded again at 8:00 h.

Compared to the cloudy day, values of VPD in a dry-season-day were twofold higher during daytime and up to five times higher in the course of the night. Sap flow was more than doubled, reaching rates of up to 41 ml min^{-1}. Total sap flow on these two days was 4.6 l d^{-1} and 10.7 l d^{-1}, respectively (Figure 34).

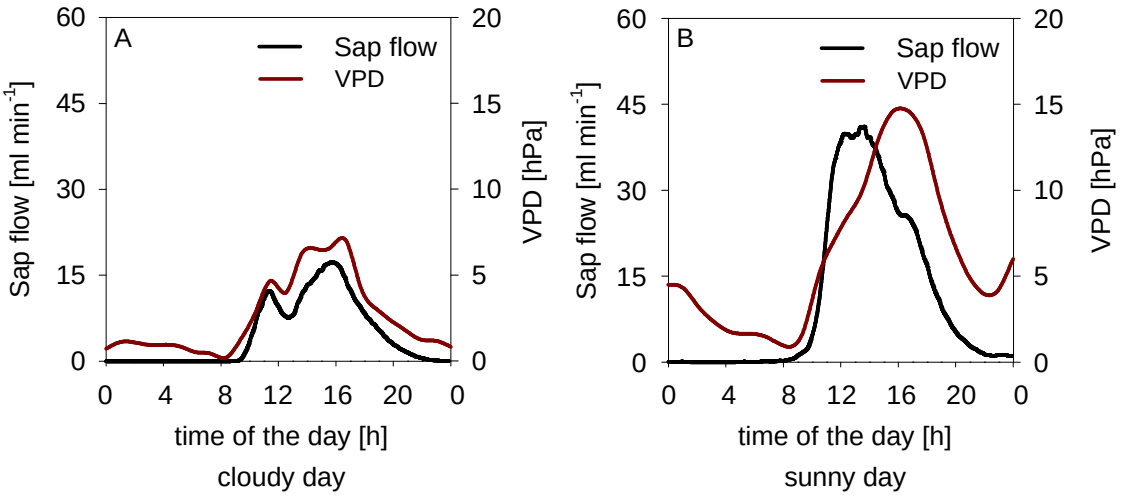

Figure 31: Relation between sap flow and VPD in the natural forest. Diurnal courses of sap flow of a small *Podocarpus falcatus* tree (dbh 8.7 cm) and of VPD. A: cloudy day (June 1, 2006) and B: dry season's day (January 22, 2007).

The diurnal courses of sap flow of the *Podocarpus falcatus* sapling in the *Pinus* plantation on two selected days are shown in Figure 32. On the rainy day sap flow (Figure 32 A) started at 10:00 h and ceased at 20:00 h. Sap flow, again interrupted by a midday depression, was peaking at a rate of approximately 18 ml min^{-1} at 16:00 h. The corresponding value of VPD was 9.3 hPa. In principle a similar relation between sap flow rates and VPD as shown above for the *Podocarpus* tree in the natural forest was recorded under the canopy of *Pinus*: On the rainy day sap flow rates paralleled VPD whereas the correlation between both diurnal courses was less close on a dry season's day (Figure 32 B) when the peak of sap flow (30 ml min^{-1} at 11:30 h) preceded that of VPD (13.5 hPa) by 6 h. Sap flow was recorded on a rainy day over 10 h while it took place over 18 h during the dry season's day. It lasted until 22:00 h in the evening while transpiration had finished about 3 h earlier. VPD remained relatively high during the whole night reaching its minimum of about 1.5 hPa shortly after sunrise.

Total sap flow on the presented days was 2.9 l d^{-1} on the cloudy day in April and 6.9 l d^{-1} on the sunny day in December (Figure 34). It should be kept in mind that the sapling under the *Pinus* canopy was considerably smaller than that in the natural forest.

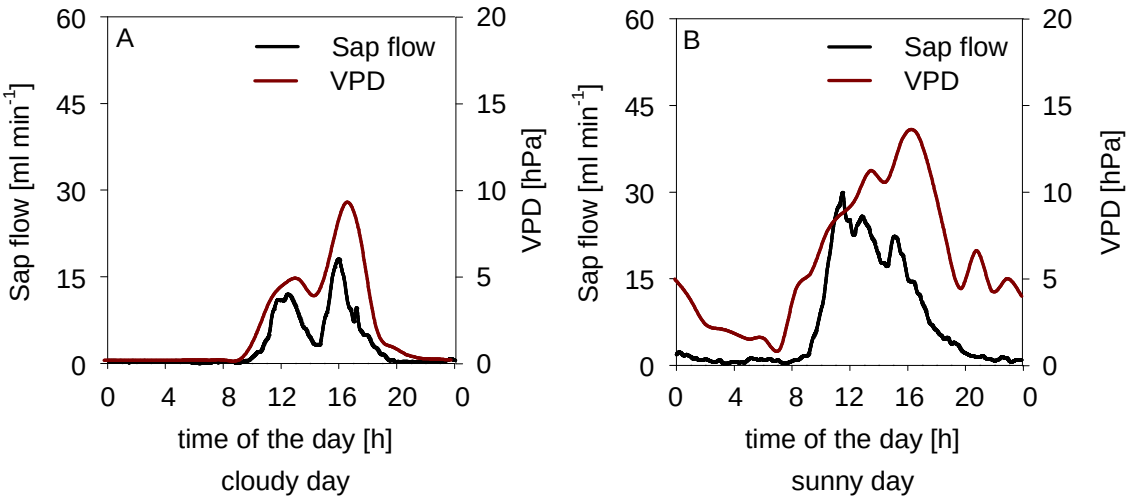

Figure 32: Relation between sap flow and VPD in the *Pinus* plantation. Diurnal courses of sap flow of a *Podocarpus falcatus* sapling (dbh 5.2 cm) and of VPD. A: cloudy day (April 9, 2006) and B: sunny day (December 15, 2006).

The same type of correlation between sap flow and VPD, as described for *Podocarpus* saplings in the natural forest and the *Pinus* plantation was also recorded with the sapling under the *Eucalyptus* canopy. On the rainy season's day, sap flow was relatively high with regard to VPD, especially in the morning hours and the midday depressions of both variables were more pronounced (Figure 33 A). The peak rate of sap flow (20 ml min^{-1}) was attained at 17:00 h when also VPD peaked (5.6 hPa). Both variables declined slowly until midnight.

In the dry season (Figure 33 B), sap flow peaked shortly before noon (41.1 ml min^{-1}) and declined gradually until 22:00 h when it became zero. VPD attained maximum from 15:00 to 19:00 h (15.3 hPa), after which it decreased with a high rate until 22:00 h and then more slowly until 8:30 h in the morning. In contrast to the situation in the *Pinus* plantation sap flow started concomitantly with the increase of VPD in the morning. Total sap flow on the presented cloudy day was 4.5 l d^{-1}. On the dry season's day it was twice as much (10.4 l d^{-1})

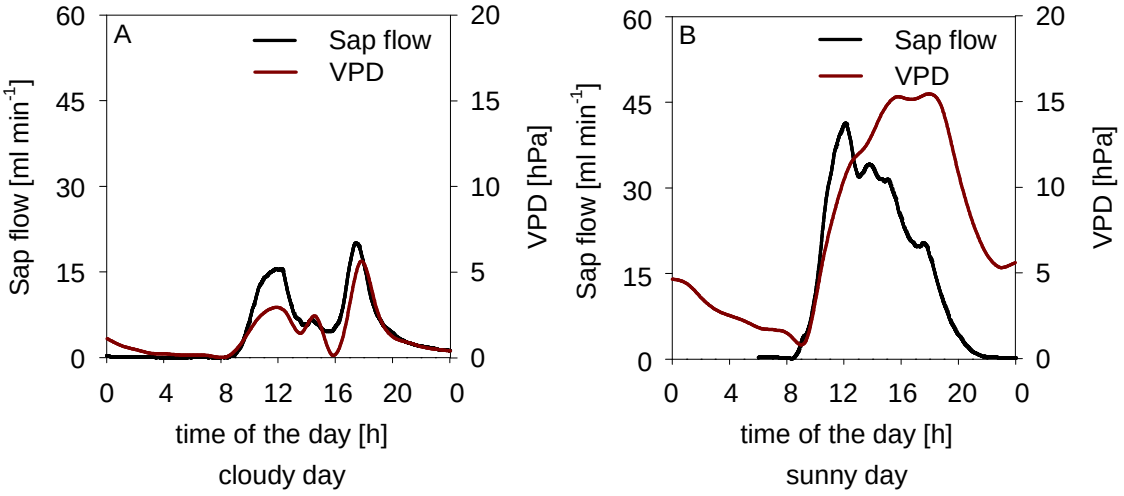

Figure 33: Relation between sap flow and VPD in the *Eucalyptus* plantation. Diurnal courses of sap flow of a *Podocarpus falcatus* sapling (dbh 8.7 cm) and of VPD. A: cloudy day (April 11, 2006) and B: sunny day (February 11, 2006).

3.6.2 Daily sums of sap flow of the *Podocarpus falcatus* saplings in the different sites on example days in the rainy and dry season

As mentioned above and shown in Figure 34, the daily sums of sap flow of the *Podocarpus* saplings differed with tree size and season. In both seasons, the two *Podocarpus* sapling in the natural forest and in the *Eucalyptus* plantation had almost identical daily sums of 4.6 and 4.5 l d^{-1}, respectively on the rainy day, and 10.7 and 10.4 l d^{-1}, respectively on the dry day. Both saplings were of comparable size with a dbh of 8.7 cm and a height of 7.6 m for the bigger sapling in the natural forest and a dbh of 8.7 cm and height of 6.3 m for the sapling in the *Eucalyptus* site. The smaller *Podocarpus* sapling in the *Pinus* site with a dbh of 5.2 cm and a height of 4.8 m had clearly lower daily sums of sap flow of 2.9 l d^{-1} on the rainy and 6.9 l d^{-1} on the dry day.

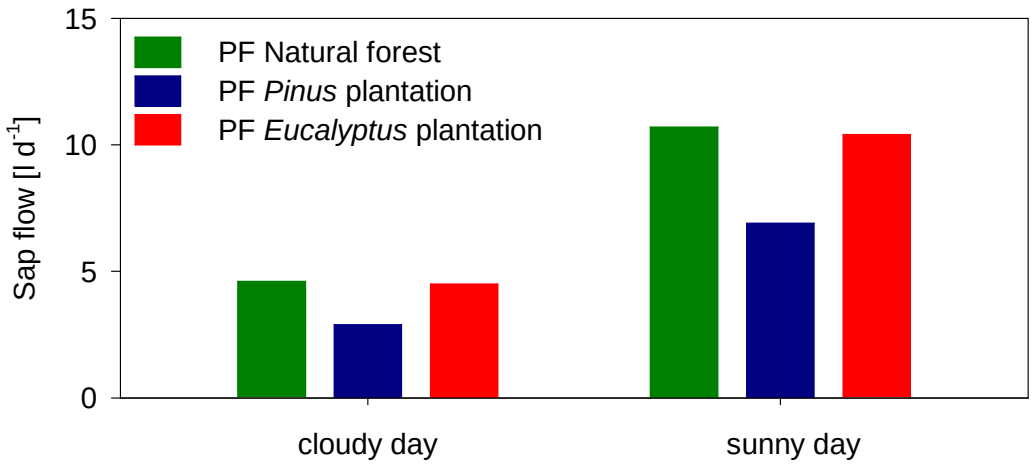

Figure 34: Daily sums of sap flow of the *Podocarpus falcatus* saplings in all 3 sites on the example days under rainy seasons conditions (cloudy day) (natural forest: June 1, 2006, *Pinus* plantation: April 9, 2006, *Eucalyptus* plantation: April 11, 2006) and dry seasons conditions (sunny day) (natural forest: January 22, 2007, *Pinus* plantation: December 15, 2006, *Eucalyptus* plantation: April 12, 2006).

3.6.3 Sap flow of the shelter-trees

The diurnal courses of sap flow of three *Podocarpus falcatus* shelter-trees are shown in Figure 35 for two days, selected to represent rainy and dry season conditions. On the rainy day (Figure 35 A), sap flow increased in all three trees at 9:00 h and ceased at 20:00 h. High flux rates were recorded between 11:00 and 16:00 h. Maximum fluxes of 18.3 and 29.9 ml min^{-1} for *Podocarpus* 2 and 3, respectively, were found around noon, whereas for *Podocarpus falcatus* 1, maximum flux (25.6 ml min^{-1}) was measured in the afternoon at 15:00 h.

On the sunny day (Figure 35 B) sap flow started also at 9:00 h but extended into the night. For the smaller of the three *Podocarpus* shelter-trees (PF 2), sap flow ended around 10:00 h, whereas the other two trees still showed stem flow until 3 o'clock in the morning. The same timing of the sap flow maximum as on a rainy day was observed under dry season condition. Thus PF 2 and PF 3 reached their maxima at noon (46.2 and 56.0 ml min^{-1}, respectively) while sap flow in PF 1 was still increasing to its maximum (54.9 ml min^{-1}) at 15:30 h.

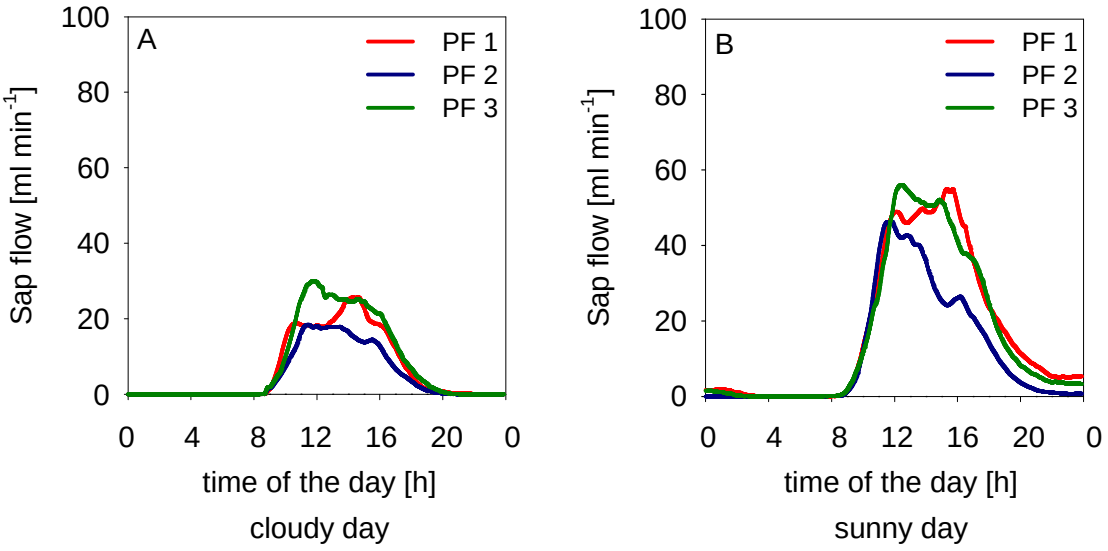

Figure 35: Diurnal courses of sap flow of 3 *Podocarpus falcatus* shelter-trees in the natural forest. A: rainy day (May 12, 2006) and B: sunny day (January 22, 2007). Dbh of the trees: PF 1: 21.7 cm, PF 2: 10.9 cm and PF 3: 22.4 cm.

Total sap flow on the two example days (Figure 36) were 9.4 and 11.1 l d^{-1} in the rainy season for the bigger trees PF 1 and PF 3, respectively, and 6.9 l d^{-1} for the smaller *Podocarpus* PF 2. In the dry season, the daily accumulated sap flow of the two bigger trees was 23.4 l d^{-1} for PF 1 and 24.4 l d^{-1} for PF 3, respectively, whereas the daily sum of *Podocarpus* PF 2 was lower (16.4 l d^{-1}).

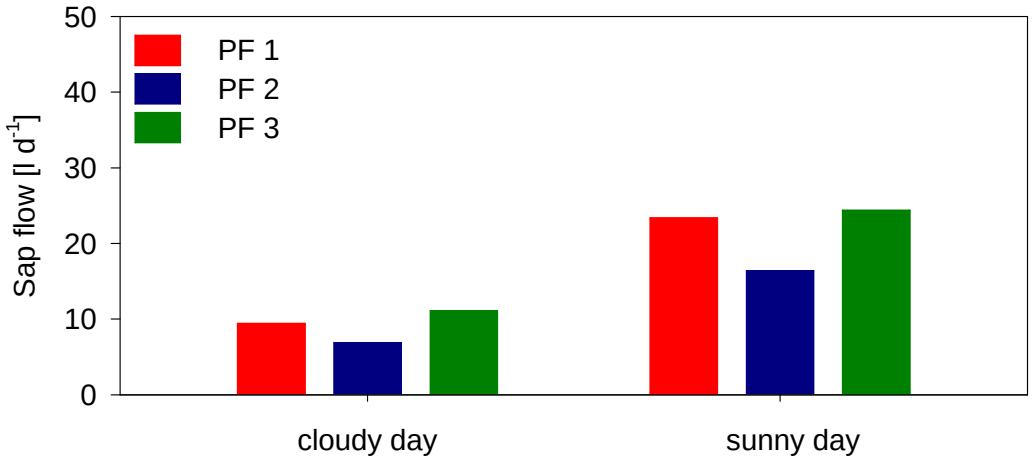

Figure 36: Daily sums of sap flow of the *Podocarpus falcatus* shelter-trees in the natural forest on the example days: cloudy day (May 12, 2006); sunny day (January 22, 2007). Dbh of the trees: PF 1: 21.7 cm, PF 2: 10.9 cm and PF 3: 22.4 cm.

The three investigated *Pinus* shelter-trees were of different size and accordingly different were the sap flow rates and amounts. Surprisingly, all 3 trees showed a pronounced midday depression of sap flow on the rainy (Figure 37 A), but not on the sunny day (Figure 37 B). While sap flow started in all 3 trees at the same time (around 8:00 h) its extension into the night correlated with the size of the tree. Flux rates were still high at 20:00 h in the biggest tree (about 10 ml min^{-1}) irrespective of the season. The total amount of daily sap flow representing the whole-tree transpiration was much higher than of the *Podocarpus* trees. *Pinus* 1 consumed 14.0 l on the rainy and 23.9 l on the sunny day. The corresponding amounts were 17.7 and 22.7 l for *Pinus* 2 and 31.9 and 43.7 l for *Pinus* 3 (Figure 38).

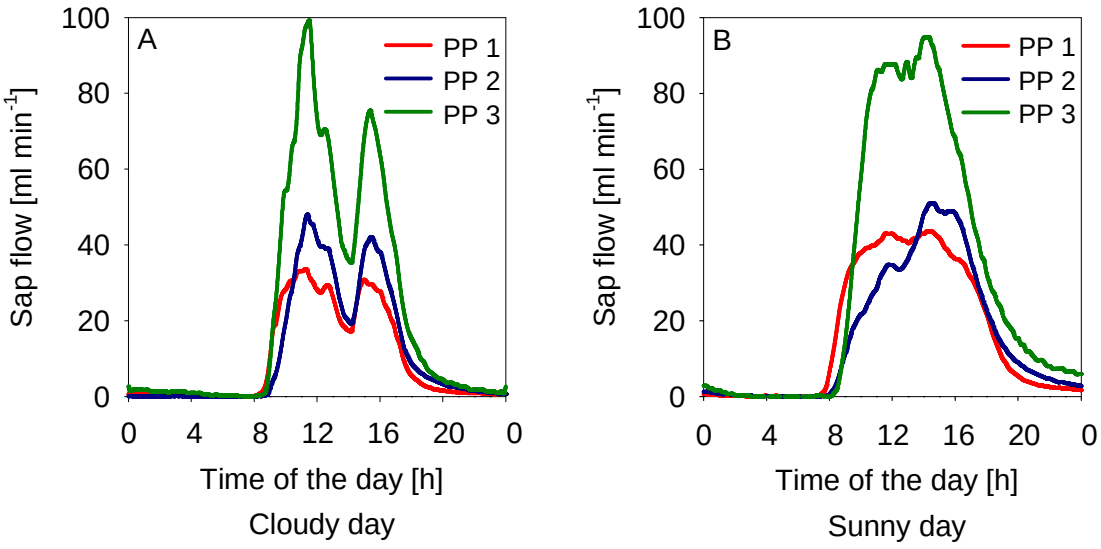

Figure 37: Diurnal courses of sap flow of 3 *Pinus patula* trees in the *Pinus* plantation. A: rainy day (April 9, 2006) and B: sunny day (December 14, 2006). Dbh of the trees: PP 1: 28.8 cm, PP 2: 35.4 cm and PP 3: 41.2 cm.

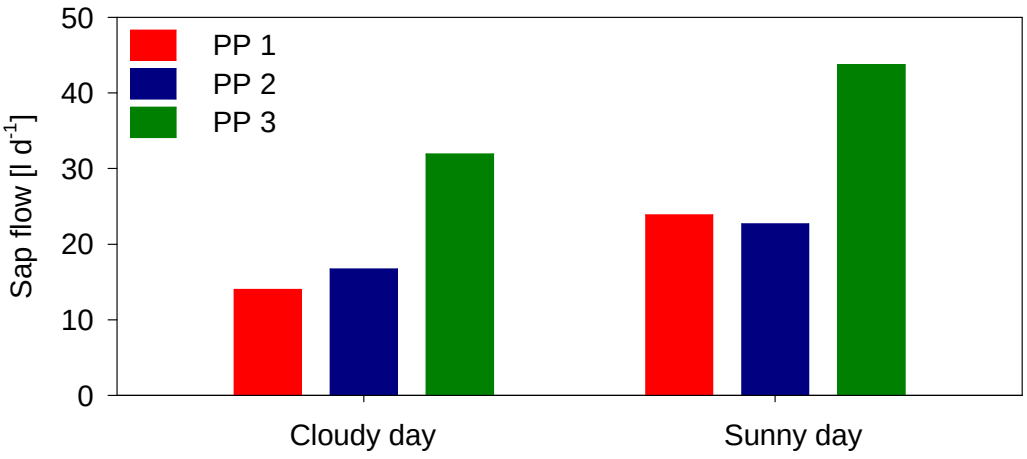

Figure 38: Daily sums of sap flow of the 3 *Pinus patula* in the *Pinus* plantation on the example days: Rainy day (April 9, 2006); sunny day (December 14, 2006). Dbh of the trees: PP 1: 28.8 cm, PP 2: 35.4 cm and PP 3: 41.2 cm.

Sap flow in the *Eucalyptus* shelter-trees differed considerably between the coppiced (ES 1, ES 2, ES 5) and the non-coppiced (ES 3 and ES 4) individuals. While the coppiced trees were of similar size (dbh between 11 and 18.5 cm) the non-coppiced shelter-trees were quite divergent (dbh 17.2 and 37.5 cm). Thus, one of the non-coppiced trees (ES) 4 was even a little smaller than the biggest coppiced individual (ES 2). Nevertheless its sap flow rates and the amount of the daily consumed water were much higher than in the otherwise comparable coppiced individual. Like in the other shelter-trees, sap flow showed a very pronounced midday depression on the rainy day which was transitorily interrupted by a short peak (Figure 39 A) but no such phenomenon occurred on the sunny day (Figure 39 B). In all coppiced individuals sap flow was low but the dynamics were the same as in the non-coppiced trees. On the dry season day a more or less bell-shaped diurnal course was observed in all trees, and unlike *Podocarpus* and *Pinus* sap flow did not extend significantly into the night hours.

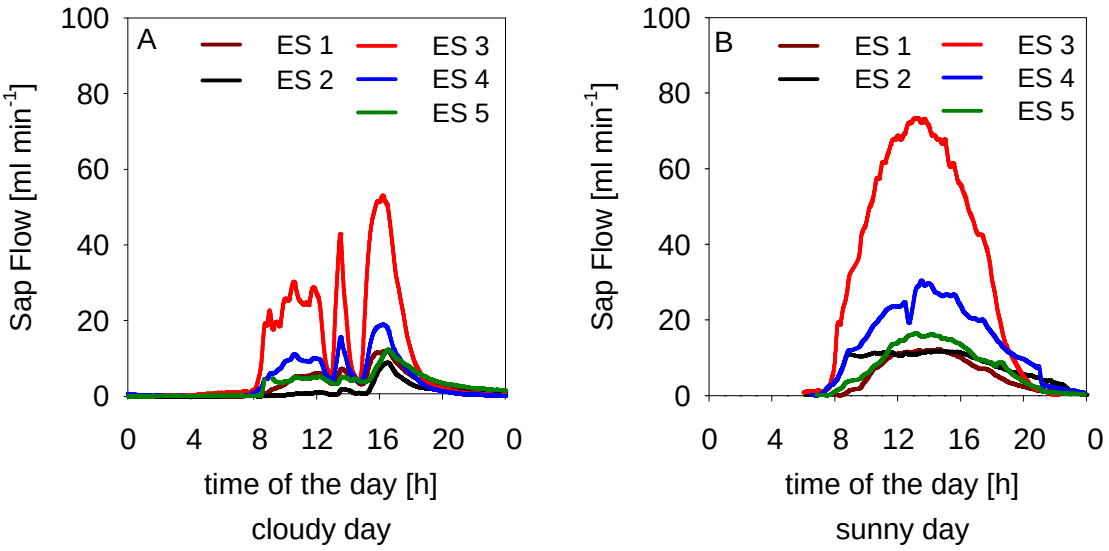

Figure 39: Diurnal courses of sap flow of 5 *Eucalyptus saligna* trees in the *Eucalyptus* plantation. A: cloudy day (April 11, 2006) and B: sunny day (February 11, 2006). ES 1, 2 and 5 coppiced, ES 3 and 4 non-coppiced. Dbh of the trees: ES 1: 17.0 cm, ES 2: 18.5 cm, ES 3: 37.5 cm, ES 4: 17.2 cm and ES 5 11.2 cm.

Eucalyptus is known as a highly water demanding tree genus. However, when compared with *Podocarpus* and *Pinus*, its water consumption was very moderate, especially so of the coppiced trees. On the rainy day the coppiced individuals consumed between 1.7 and 5.3 l d^{-1} and on the sunny day between 5.4 and 7.4 l d^{-1}. The non-coppiced smaller ES 4 consumed 8.6 and 13.9 l d^{-1} during the rainy and the sunny day, respectively. Higher water demand was calculated for the big non-coppiced ES 3 whose total water consumption was 19.1 and 32.7 l d^{-1} on the rainy and the sunny day, respectively (Figure 40). Comparison of *Podocarpus* 3 (22.4 cm dbh) and *Pinus* 1 (28.8 cm dbh) with *Eucalyptus* 4 (17.2 cm dbh) which with regard to size were the most similar individuals of the investigated shelter-trees, shows that *Eucalyptus* (8.6 l d^{-1} and 13.9 l d^{-1}) consumed less water per day than *Podocarpus* 3 (11.1 l d^{-1} and 24.4 l d^{-1}) and *Pinus* 1 (14.0 l d^{-1} and 23.9 l d^{-1}). Comparing the two biggest shelter-trees *Pinus* 3 (41.2 cm dbh) and *Eucalyptus* 3 (37.5 cm dbh), *Pinus* was again consuming 30% more water in the rainy and dry season (31.9 and 43.7 l d^{-1}), respectively, as compared to the big *Eucalyptus saligna (*19.1 and 32.7 l d^{-1}).

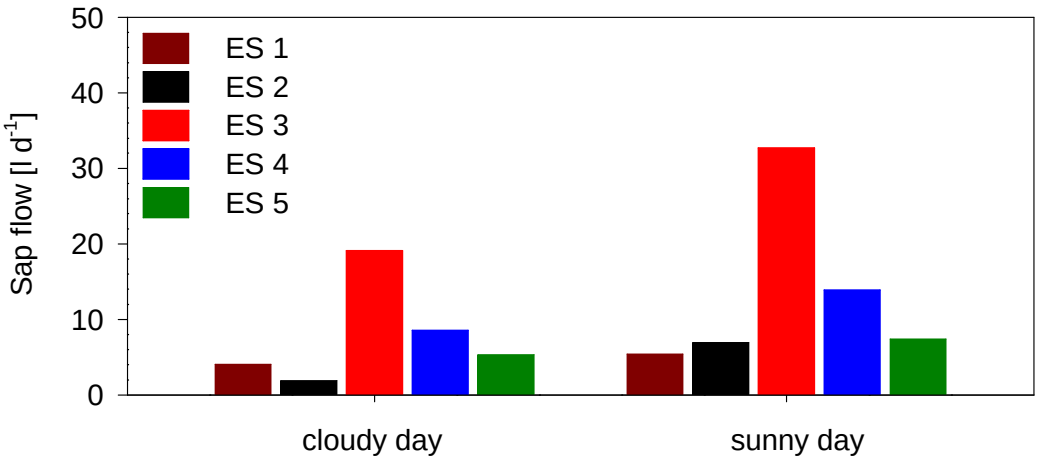

Figure 40: Daily sums of stem flow of 5 *Eucalyptus saligna* trees in the *Eucalyptus* plantation on a day in the rainy season (April 11, 2006) and on a sunny day in the dry season (February 11, 2006). Dbh of the trees: ES 1: 17.0 cm, ES 2: 18.5 cm, ES 3: 37.5 cm, ES 4: 17.2 cm and ES 5 11.2 cm.

3.6.4 Daily sums of sap flow of the *Podocarpus* saplings and shelter-trees

Comparison of the daily sums of sap flow of all trees is shown in Table 9. Of all trees, daily sap flow was higher in the dry season compared to the rainy season, although for the *Eucalyptus* shelter-trees, this difference was not statistically significant. The *Podocarpus* saplings nearly doubled sap flow in the dry season (ranging from 3.6 to 9.6 l d^{-1} in the rainy season and from 8.3 to 14.0 l d^{-1} in the dry season, respectively, n = 134, $p < 0.001$).

Of all the shelter-trees, *Pinus patula* had the highest daily sums of sap flow. Values for all measured pine trees were 11.6 to 20.4 l d^{-1} on rainy days and between 19.3 and 33.3 l d^{-1} on sunny days (n = 66, $p < 0.001$). The *Podocarpus falcatus* shelter-trees showed the biggest difference in sap flow between the rainy and the dry season. On rainy days, mean daily sum ranged between 7.2 and 8.8 l d^{-1}, whereas in the dry season, values were more than twice as much (15.9 to 21.8 l d^{-1}, n = 279, $p < 0.001$).

For the *Eucalyptus saligna* shelter-trees, daily sums of sap flow were considerably lower for the coppiced trees (1.2 to 3.8 l d^{-1} and 3.9 to 6.3 l d^{-1} in the rainy and dry season, respectively) as compared to the non-coppiced trees (5.6 to 21.3 l d^{-1} in the rainy season and 11.0 to 27.6 l d^{-1} in the dry season, respectively).

Table 9: Daily sums of sap flow of all investigated trees on cloudy and sunny days (mean sums, and number of examined days). *PF*: *Podocarpus falcatus*, *PP*: *Pinus patula*, *ES*: *Eucalyptus saligna*; NF: natural forest, PP: *Pinus* plantation, ES: *Eucalyptus* plantation

Tree (dbh)	Sap flow [l d^{-1}] cloudy days	Sap flow [l d^{-1}] sunny days
Saplings		
***PF* NF (8.7 cm)**	5.9 (29 days)	10.0 (60 days)
***PF* PP (5.1 cm)**	3.6 (11 days)	8.3 (11 days)
***PF* ES (8.7 cm)**	9.6 (3 days)	14.0 (4 days)
Shelter-trees		
***PF* 1 (21.7 cm)**	7.8 (29 days)	21.8 (64 days)
***PF* 2 (10.9 cm)**	7.2 (29 days)	15.9 (64 days)
***PF* 3 (22.4 cm)**	8.8 (29 days)	19.7 (64 days)
***PP* 1 (28.8 cm)**	11.6 (11 days)	19.3 (11 days)
***PP* 2 (35.4 cm)**	13.0 (11 days)	25.9 (11 days)
***PP* 3 (41.2 cm)**	20.4 (11 days)	33.3 (11 days)
***ES* 1 (17.0 cm), coppiced**	3.5 (3 days)	5.4 (4 days)
***ES* 2 (18.5 cm), coppiced**	1.2 (3 days)	3.9 (4 days)
***ES* 3 (37.5 cm), non-coppiced**	21.3 (3 days)	27.6 (4 days)
***ES* 4 (17.2 cm), non-coppiced**	5.6 (3 days)	11.0 (4 days)
***ES* 5 (11.2 cm), coppiced**	3.8 (3 days)	6.3 (4 days)

3.6.5 Transpiration *versus* sap flow

Transpiration and sap flow, although representing physiologically connected parameters, are expressed in different nominal dimensions and thus can only be correlated in terms of the daily dynamics. Sap flow provides a measure of the total transpired water, whereas transpiration is related to a normalized transpiring area. Transpiration follows more closely the daily course of VPD whereas the rate of sap flow is temporally buffered by the amount of water stored in the conducting tissue of the axes. Daily courses of VPD, transpiration, stomatal conductance and sap flow of a *Podocarpus falcatus* sapling in the *Pinus* forest are shown in Figure 41 A and B and of a *Pinus patula* shelter-tree in Figure 42 A and B for a rainy and a dry-season day. While the daily course of transpiration follows in general that of VPD on both the sunny and the rainy day (in the morning hours more closely than in the afternoon) and for both trees, the kinetics of sap flow differed in three respects: i) The relation of the size of the peaks

differed considerably from the relation of the peaks in transpiration, ii) the dynamics of peaks and minima was delayed by about 1 h with respect to that of transpiration, and iii) sap flow continued into the night whereas transpiration ceased shortly after sunset. While on the rainy day transpiration and sap flow started simultaneously in the morning, on the sunny day onset of sap flow was delayed by one hour indicating some xylem sap reserves in the stem which supplied the initial transpiration. Replenishment of that store took place during the night hours when transpiration was more or less zero. The increase in sap flow in the morning of the rainy day was much faster than under dry season conditions and the transpiration rates were also slightly higher than on the sunny day, indicating some stomatal limitation already in the morning. Again a strong midday depression of sap flow and transpiration was recorded on the rainy day as a result of the decrease of VPD and light intensity (data not shown) due to heavy clouds coming up in the course of the morning. As a result of upcoming rain in the evening (starting at 16:45 h), stomata were closing and transpiration stopped.

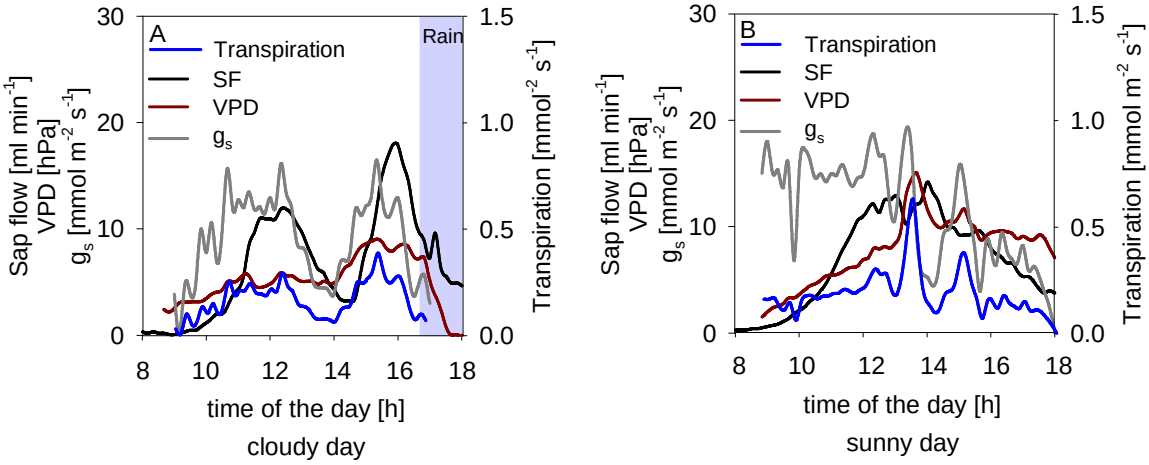

Figure 41: Diurnal courses of sap flow (black), transpiration (blue) and stomatal conductance (g_s, grey) of a *Podocarpus falcatus* sapling, and VPD (dark red) in the *Pinus* plantation. A: rainy season day (April 9, 2006) and B: sunny day (December 13, 2006). Dbh of the sapling (PP *PF* 1): 5.2 cm.

Concerning the kinetics, the daily course of the *Pinus* shelter-tree were quiet similar to those of the *Podocarpus* sapling. Starting point of sap flow was, like in the sapling, at the same time as transpiration on the cloudy day and started with one hour delay on the day with sunny weather conditions. The increase of sap flow was also faster on the rainy day, but transpiration rates were higher on the sunny day of the *Pinus* shelter-tree. In contrast to the *Podocarpus* sapling, a midday depression in sap flow could not be observed.

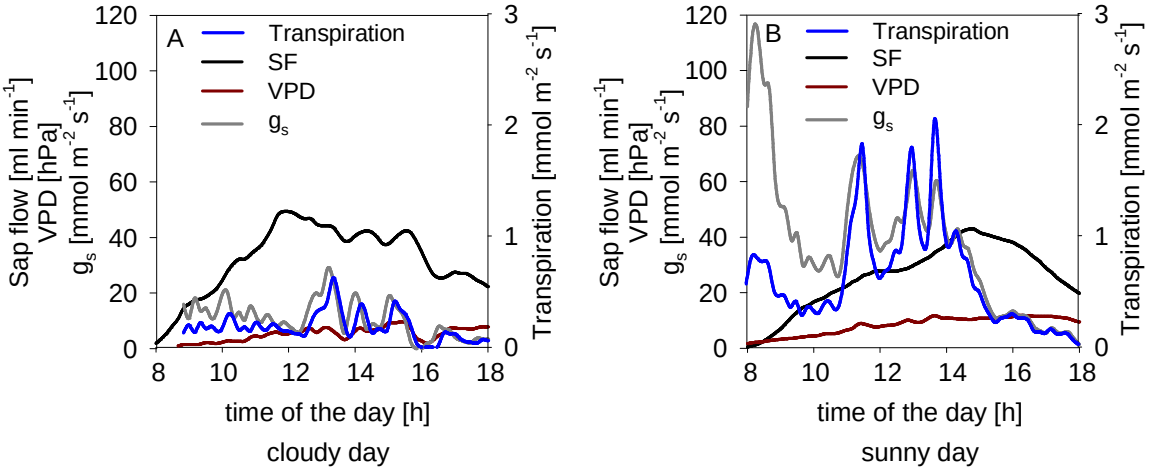

Figure 42: Diurnal courses of sap flow (black), stomatal conductance (grey) and transpiration (blue) of a *Pinus patula* shelter-tree, and VPD (dark red) in the *Pinus* plantation. A: cloudy day (April 10, 2006) and B: sunny day (December 14, 2006). Dbh of the tree PP 1: 28.8 cm.

3.7 Carbon isotopes (δ ^{13}C) of the leaves of the *Podocarpus falcatus* saplings and nurse-trees

δ ^{13}C values of leaf tissue are commonly used to characterize the long term water relations of a plant, taking in consideration the general difference between the slightly discriminating C4-type and strongly discriminating C3-type photosynthesis. All tree species investigated in this study perform C3-type photosynthesis characterized by an average isotope ratio of 30‰. Slightly higher discrimination indicates long-term high stomatal conductivity and *vice versa* (Scheidegger et al. 2000). *Podocarpus* produces its leaves during the rainy season (Yigremachew Lemma, personal communication) when the water relations of the trees are relaxed. Therefore in addition to the usually examined mature leaves the δ ^{13}C values of young leaves were analysed to assess the statement of the ^{13}C discrimination values.

δ ^{13}C values of young and mature leaves of the same tree were virtually identical and close to 30‰ except the mature leaves from saplings in the *Pinus* plantation which were slightly lower (Table 10). Although the difference to the other values was statistically not significant, it might indicate some water shortage during the dry season. Significantly differing ($p < 0.001$) δ ^{13}C values were found between *Pinus patula* shelter-trees and all other trees ($n = 18$, $p < 0.001$) except *Eucalyptus* ($n = 18$, $p = 0.08$); and between the *Podocarpus falcatus* shelter-trees and the saplings under the natural ($n = 18$, $p = 0.03$) and the *Eucalyptus* canopy ($n = 18$, $p = 0.01$), respectively. Of all trees

Podocarpus falcatus shelter-trees showed the highest (-28.8 ‰) and *Pinus patula* the lowest (-31.0 ‰) values indicating permanently relaxed water relations of the *Pinus* shelter-tree and at least temporary water stress on the *Podocarpus* shelter-tree.

Table 10: δ ^{13}C isotope ratios of leaves of *Podocarpus* saplings and adult shelter-trees. Numbers represent means of three trees with a sample size of three bulk samples of young and mature leaves and standard error. Different letters indicate significant differences between the leaves.

Trees	δ ^{13}C values of young leaves (*n* = 9) [‰]	δ ^{13}C values of mature leaves (*n* = 9) [‰]
Podocarpus saplings (natural forest)	-29.5 ± 0.2^{a}	-29.4 ± 0.3^{a}
Podocarpus saplings (*Pinus* plantation)	-29.4 ± 0.3^{ab}	-28.6 ± 0.4^{ab}
Podocarpus saplings (*Eucalyptus* plantation)	-29.3 ± 0.3^{a}	-29.6 ± 0.4^{a}
Podocarpus shelter-tree	-28.8 ± 0.1^{b}	-28.7 ± 1.3^{b}
Pinus patula shelter-tree	-31.0 ± 0.2^{c}	-31.1 ± 1.2^{c}
Eucalyptus saligna shelter-tree	-29.3 ± 0.6^{abc}	-30.1 ± 3.0^{abc}

4 Discussion

This work focuses on growth of young *Podocarpus falcatus* trees, in the context of the natural rejuvenation of *Podocarpus falcatus* in three different forest types of the Munessa-Shashamene Forest (Strobl et al. in press)(cf. Strobl et al. in press). Considering only natural regeneration, the study had to use young trees which were not uniform in size and age and grew at various densities in the three forests (Feyera et al. 2002). However, effects of densities, i.e. distance of the individual saplings were not in the focus of this study. This study rather concentrates on the growth of the *Podocarpus* saplings under the three different canopies of the shelter-trees which according to several other authors (Parrotta 1992; Fimbel and Fimbel 1996; Parrotta 1997; Fetene and Feleke 2001; Feyera et al. 2002; Luettge et al. 2003; Fetene and Beck 2004) should be better under *Eucalyptus* and *Pinus* than under the canopy of the natural *Podocarpus* mixed forest. To analyse this unexpected observation with saplings of different age and size a detailed study of the sub-canopy microclimates was performed, in order to comprehend differences in the microenvironment of the young trees which could explain different growth rates. As response to the respective microclimates, photosynthesis and water relations of the saplings were studied.

4.1 Verification of the shelter-tree effect on the growth of *Podocarpus* saplings

First of all, the reported growth-stimulating nurse- or shelter-tree effects had to be verified, using the natural *Podocarpus* forest as control situation. Growth was measured as relative growth rates of the stem diameter, although this measure is subject to further modifications: First, especially with respect to the different size of the saplings , it is strongly depending on the age of the young trees, as reported by several authors (Brienen and Zuidema 2006; Martínez-Vilalta et al. 2007). Secondly it depends on the size of the crowns of the saplings. Since LAI is not a useful measure of the crown under the canopy of shelter-trees another proxy was introduced to represent the crown size: The crown projection area (Figure 8). Highest relative growth rates with and without the correction by the crown size were found for the *Podocarpus* saplings under the shelter of *Pinus patula*. Uncorrected RGR was only slightly higher under *Eucalyptus* than under the natural canopy, however, when corrected by the proxy for the crown size (Table 11),

it was less than half of it. As a result, for the observation period of 2 years, the positive shelter-tree effect could only be confirmed for the *Pinus* plantation.

Table 11: Relative diameter (at breast height) growth rates (RGR), crown projection areas (CPA) and ratio of RGR and CPA of the *Podocarpus* saplings in the three different forest sites. Numbers given for RGR and CPA are means with standard errors (natural forest: *n* = 5, *Pinus* plantation: *n* = 9, *Eucalyptus* plantation: *n* = 7). Lowercase letters indicate significant differences between the sites.

	Natural forest	***Pinus* plantation**	***Eucalyptus* plantation**
RGR [mm cm^{-1} $month^{-1}$]	0.08 ± 0.02^{a}	0.30 ± 0.06^{b}	0.09 ± 0.02^{a}
CPA [m^2]	2.6 ± 1.1	3.7 ± 0.4	7.9 ± 2.1
Normalized RGR/CPA [mm cm^{-1} $month^{-1}$] [m^{-2}]	0.03	0.08	0.01

Are the reports of a positive “nurse-tree effect” of *Eucalyptus* on the growth of *Podocarpus* saplings (Senbeta et al. 2002; Yirdaw and Luukkanen 2003; Selwyn and Ganesan 2009; Teshome 2009) wrong? For a fair assessment of the situation, it is necessary to consider the management practices of the natural forest and the exotic plantations by the owners of the forest (Forest Enterprise, Arsi Negele, Ethiopia). Theoretically, the natural forest is a protected area where it is not allowed to fell trees, but due to the high demand of firewood (Pohjonen and Pukkala 1990) and the selective logging by local people and cattle grazing (Krepkowski et al. 2011), the forest is highly disturbed. Although *Podocarpus* is not affected by herbivores (Tesfaye et al. 2002), the general lower number of saplings and trees in the natural forest can be attributed mainly to human disturbances such as cutting of trees for different uses (Teketay 1997b; Teketay 1997a; Senbeta and Teketay 2001). The plantations are protected by guards against illegal logging, and grazing is restricted at least in younger plantations.

Pinus plantations are usually clear-cut after 25 to 30 years, with periodic thinning once in a while, whereas *Eucalyptus* plantations are usually coppiced in intervals of 5 - 7 years (Feyera et al. 2002; Tadele 2004). This short rotation system results in a largely changing light climate for the undergrowth (Feyera et al. 2002). In related studies, a higher density and a better regeneration of native woody plants was found in coppiced stands of *Eucalyptus saligna* compared to the natural forest and conifer plantations (Michelsen et al. 1996; Senbeta et al. 2002), where a better light climate for the saplings is provided by the *Eucalyptus* canopy due to its better light regime caused by a less dense crown. The density of the crowns in the *Eucalyptus* plantation changes

considerably with the time after the last coppicing. The *Eucalyptus* plantation of the study site in the Munessa forest was coppiced at least once, but more likely two or three times as estimated from the age (31 years) and height of overtopping individuals (35 – 40 m). The height of the young *Eucalyptus* trees (12.6 and 26.0 m) which had sprouted from the rootstocks after coppicing indicate at least a time span of 7 years for the smaller and 15 for the bigger coppice, considering the reported growth rates of *Eucalyptus saligna* (Whitesell et al. 1987), at the region. Due to coppicing the canopy of the investigated *Eucalyptus* site was at least two-tiered with a patchy upper layer of the crowns of the uncoppiced and a lower layer formed by the crowns of the re-sprouted trees. Coppicing changes the light regime of the undergrowth fundamentally from shade into a high-light situation and photosynthetic CO_2 net uptake from light limitation to light saturation. This in turn stimulates growth as long as the *Podocarpus* saplings are not overtopped by the faster growing new *Eucalyptus* shoots. As our investigations took place some years after the last coppicing, the saplings in the *Eucalyptus* site were considerably shadowed and thus in the state of reduced growth which will turn into maximum growth rates after the next coppicing. Whereas the *Podocarpus* saplings in the natural forest and under the shelter of *Pinus* grow more or less continuously, those in the *Eucalyptus* plantation show intermittent growth following the changes in the light climate.

Therefore, a longer observation period under the canopy of *Eucalyptus* is required, that encompasses the reaction of the *Podocarpus* saplings to the common practice of coppicing of the shelter-trees.

Interestingly, growth rates of the saplings did not differ significantly during the wet and the dry seasons. Although daily water consumption as measured by total sap flow was considerably higher on days of the dry season than on rainy days (Table 9), stronger limitation of transpiration by drought-induced stomatal closure (Lloyd and Farquhar 2008) could not be detected during the dry season. On the contrary, reduced sap flow could be attributed to a low VPD rather than to a shortage of water supply to the young as well as to the shelter-trees (Verbeeck et al. 2007).

4.2 Influence of climate factors on the performance and water relations of the *Podocarpus* saplings

Light and VPD were the most effective abiotic variables controlling photosynthetic net CO_2 uptake by the *Podocarpus* saplings (cf. 3.4.1 Investigation of factors influencing

CO_2 net uptake). Since growth models based on daily sums of radiation and stomatal conductance are not available for *Podocarpus*, photosynthetic CO_2 assimilation was used as a proxy for biomass production and growth. It is responding to the intensity of PAR, but limited by temperature and stomatal conductance. Correlation analysis indicated that 71% of the daily carbon gain resulted from response to PAR while only 4% could be attributed to VPD- and temperature effects. The remaining 25% which could not be traced to specific environmental factors may have resulted from limitation through stomatal conductance and from combinations of the variables.

4.2.1 Temperatures and VPD

In the annual course of the microclimate, monthly means of the climate factors temperature and VPD showed that in both plantations, but especially in the *Pinus* site, conditions were drier compared to the natural forest which could be detrimental for the recruitment of seedlings (Krepkowski et al. 2011). Air temperature was up to 1.8 ℃ higher in both plantations, but higher VPD could only be observed in the *Pinus* plantation in the dry season. In the daily courses, air temperatures, ranging between a minimum of 4 ℃ usually at or shortly after sunrise and a maximum of 26 ℃ in the afternoon could affect photosynthetic net carbon gain; but during the daily hours, when photosynthesis is possible, the air temperatures were in a range where small differences as recorded between the 3 sites are of less importance; super-optimal temperatures occurred only during a short time period (1 - 2 hours) at noon. Rather air temperatures affect photosynthetic CO_2 uptake via VPD (Comstock 2002) which in the afternoon resulted in a partial closure of the stomata (Figure 28). The daily courses of VPD also indicated a drier climate in the plantations compared to the natural forest. Dry season values of VPD where higher in the *Pinus* plantation during the whole day, whereas in the *Eucalyptus* site VPD exceeded that in the natural forest only in the afternoon. Highest hourly means in the plantations during the dry season were already in a range which could affect the photosynthetic CO_2 uptake of the saplings by stomatal closure (Diaz-Espejo et al. 2007).

4.2.2 Throughfall

Monthly throughfall was similar in all sites, but during single heavy rain events, a higher maximal throughfall was measured in the natural forest. Throughfall depends on many factors, such as the structure and density of the canopy, intensity and distribution of the

rainfall events, wind speed, VPD of the air and the proportion of surface stemflow (Crockford and Richardson 2000). Interception ranges between 8.9 and 39% and stemflow between 0.1 and 13% in tropical and subtropical forests (Crockford and Richardson 1990). Canopy cover in the three sites was calculated as percentage of the projected crown area in relation to the ground area (Roehle 1986). Crown area projection of the plantations was similar with 68% for *Pinus* and 72% for *Eucalyptus*, whereas in the natural forest, the canopy was closed (99% coverage) with largely overlapping crowns. In the plantations, throughfall was not homogenous because of the patchy canopy with bigger gaps. For gap areas, 70% of gross precipitation could be added (Asdak et al. 1998) to the amounts of throughfall. Considering this, throughfall in the plantations matches the amount of throughfall in the natural forest, and consequently water supply is similar in all sites. Therefore, drier conditions, especially in the *Pinus* plantation, are not caused by lower throughfall, but rather by higher temperatures and VPD.

4.2.3 Sub-canopy light relations (PAR)

The experimental simulation of the microclimate (Figure 24) showed that the most crucial factor for carbon uptake and therefore also for the growth of the saplings is the light regime under the three different canopies. The monthly average of daily accumulated PAR outside the forest ranged from 17 mol m^{-2} d^{-1} in the rainy to 41 mol m^{-2} d^{-1} in the dry season, but losses in irradiance upon passage through the canopy were extremely high as only 0.8% (natural forest), 2.6% (*Pinus* plantation) and 3.4% (*Eucalyptus* plantation) of the outside PAR reached the saplings level. Those values are in good agreement with values reported for a tropical lowland rain forest of Costa Rica (Chazdon and Fetcher 1984), for Californian redwood forests (Pearcy and Pfitsch 1994), and a mixed coniferous-deciduous forest in New England (Canham et al. 1994).

Values of PAR measured by the microclimate stations in the three sites were 3 to 4 times higher in the plantations compared to the natural forest (Table 3), but PAR measured on selected days with the quantum sensor of the porometer in the *Eucalyptus* plantation showed lower PAR intensity compared to the other two sites (Table 7). This discrepancy between the measurements might be mainly attributed to the fact that the sensors of each microclimate station were fixed on a place in the plot representing a typical shelter-tree situation with the respective light regime of each site. In the *Eucalyptus* plantation, PAR values of the sensors of the microclimate station and of the porometer were in good agreement, whereas in the other two sites, values measured

with the porometer were significantly higher than those recorded by the microclimate stations. The major reason for the difference was the accidental distribution of the *Podocarpus* saplings in the plots (Figure 8) in relation to the selected position of the microclimate stations. Although the crown cover in the natural forest was 99%, light intensities could differ between 1 to 77% of the outside light within the site (Feyera et al. 2002) even on a small scale. Accordingly the measurements of the PAR sensor of the porometer showed not an even distribution of the radiation over the plot as could have been presumed from the microclimate stations data. The same could be observed for the *Pinus* plantation where the patchiness of the canopy leads to an uneven distribution of the light intensities within the plot, and although *Podocarpus* is a shade tolerant species (Teketay 2011), rejuvenation recruitment of the saplings is less successful in the deep shade.

4.2.4 Stomatal responses to microclimate factors and effects on CO_2 uptake

The photosynthetic response is usually more or less constrained by stomatal conductance (Dengel and Grace 2010). Stomatal movements respond to signals from the roots, from light and from the atmospheric water vapour deficit (Comstock 2002). Since stomatal conductance is calculated from transpiration and VPD, the relation between stomatal conductance and VPD is auto-correlated and therefore not independent. Measurements of the root signal was beyond the possibilities of the present work; therefore only the correlation between changes in stomatal conductance and changes in the light intensities could be examined (Table 8). In general, only weak correlations were found, the strength of which differed between the three forest types: In the natural forest and *Eucalyptus* plantation, light intensities had almost no influence on stomatal conductance of the leaves of the *Podocarpus* saplings ($r^2 = 0.19$; $n = 17$ and $r^2 = 0.13$; $n = 18$, respectively), while in the *Pinus* plantation some effect was indicated by the correlation factor of $r^2 = 0.28$ ($n = 22$). Considering that light intensities are generally higher in the *Pinus* plantation compared to the other two sites, it is not surprising that the influence of PAR on stomatal conductance is more obvious in this type of forest. The daily course of carbon uptake and the corresponding climate factors, measured with a *Podocarpus* sapling in the *Pinus* plantation (Figure 28 c and d), shows a typical example of limitation of photosynthesis by other ambient factors, most probably stomatal resistance, than light. High radiation and concomitantly high VPD could cause stomatal closure (Grace et al. 1975; Urban et al. 2007), what is indicated at all three sites by a

better correlation between stomatal conductance and PAR in the second half of the day caused by higher PAR intensities throughout noon. Accordingly, the influence of stomatal conductance on carbon uptake is higher in the afternoons, whereas the correlation between PAR and CO_2 net uptake is slightly closer in the morning hours, when temperatures and relative humidity are still not in ranges which could cause stomatal closure.

Slow diffusion (low g_s) limits CO_2 assimilation and simultaneously decreases ^{13}C discrimination (Broadmeadow et al. 1992). The slightly higher ^{13}C values of the mature leaves of the *Podocarpus* saplings in the *Pinus* plantation suggest an overall lower stomatal conductance (Scheidegger et al. 2000) over longer periods.

4.2.5 Effect of PAR on carbon uptake

As it turned out that PAR is the most influential factor for carbon uptake, the effect of varying PAR intensities on the potential performance of the saplings in the different sites was examined by measuring light response curves of CO_2 uptake (Luettge et al. 2003). For the comparison of the utilization efficiency of sunflecks for photosynthetic carbon gain in contrast to diffuse light conditions, an experimental simulation of lightflecks was carried out (Kueppers et al. 1996).

4.2.5.1 Light response curves

In all cases, the light response at low PAR intensities was higher with saplings inside the three forest types than that measured outside, indicating a reduced quantum efficiency of the leaves of the *Podocarpus* saplings growing under full sun (Figure 25). Similar results were found for tropical, temperate and boreal forests by other authors (Gu et al. 1999; Gu et al. 2002; Alton et al. 2007; Dengel and Grace 2010). Photosynthetic carbon uptake at low PAR intensities was highest in the *Eucalyptus* site, showing that *Podocarpus* can adapt to the particular environmental condition (Luettge et al. 2003), in this case to the lower light intensities occurring in the *Eucalyptus* plantation.

In contrast, the light response curve of the *Podocarpus* shelter-tree (Figure 29), measured on sun-leaves at the edge of the crown, did not show any reduction in quantum efficiency. Values for carbon uptake were higher, although saturation was already reached around 750 µmol m^{-2} s^{-1}. Identical performance of all measured leaves from the sun crown indicated that the leaves of the shelter-tree were well adapted to the high light conditions.

The measured light response curves under constant ambiental conditions differed from the optimum curve with varying temperature, VPD and rh (Figure 24). While the artificial light response curves showed saturation around 1250 µmol quanta m^{-2} s^{-1} which did not change at higher light intensities, the light response under ambiental conditions decreased at the highest intensities (2000 µmol quanta m^{-2} s^{-1}). This reflects the natural situation where at such high irradiation air and leaf temperature increase while relative humidity decreases. Under natural conditions, an increase in radiation can lead to decreases in photosynthesis because of elevation of the temperature (Gu et al. 2002). With increasing temperature VPD increases and as a consequence stomatal conductance decreases, limiting photosynthesis.

4.2.5.2 Lightflecks[2]

In nature, light is one of the most fluctuating ambient parameters, especially in half shade, where lightflecks occur (Kueppers et al. 1999). The effect of the varying light intensities on photosynthesis of the young *Podocarpus* trees was examined by simulating lightflecks with the artificial light source of the porometer at otherwise constant ambient conditions. Pre-illuminated leaves were used fort that experiment in order to simulate natural conditions. Photosynthetic carbon uptake responded with a delay of 8 - 10 s to the increase of the light intensity and returned to the low-light level about 40 s after the lightfleck (Figure 26 b). The fast response and a time lapse of only a few seconds until the maximum CO_2 uptake was achieved indicated that the leaves were in the photosynthetically active state (Pearcy 1990; Pearcy and Pfitsch 1994) when the simulation experiment started. PAR intensities used for lightfleck simulation were only 200 and 400 µmol m^{-2} s^{-1}, and because of these low intensities the post-illumination burst (Pearcy 1990) was only small. The response of carbon uptake to the lightfleck intensity matched the light response curve (Figure 25) as assimilation triggered by 400 µmol m^{-2} s^{-1} lightflecks was only 1.18 times higher as from a lightfleck at 200 µmol m^{-2} s^{-1}. The corresponding relation from the light response curve (Figure 25) is 1.16 and therefore in fair agreement with the measured value. In another part of the experiment photosynthetic efficiency of intermittent lightflecks was compared to an identical amount of PAR that was given as constant diffuse illumination over the same time period (Figure 26 a). Whereas the applied PAR intensity of 83 µmol m^{-2} s^{-1} and the basic illumination in

[2] The term “lightfleck“ is used for a high intensity light pulse from an artificial light source, while the term “sunfleck“ is reserved for a light pulse from sunlight occurring under natural conditions.

the lightfleck experiment (40 µmol m^{-2} s^{-1}) were within the linear range of the light response curve, the lightfleck intensities (200 and 400 µmol m^{-2} s^{-1}) extended into the non-linear range. Efficiency of such lightflecks was lower than that of the basic diffuse PAR intensity. A comparable experiment (Leakey et al. 2002) at higher light intensities but still within the linear range of the light response showed the same result. Likewise, if the daily sums of assimilation from the diurnal courses were related to either the daily accumulated PAR in the actual sunfleck pattern or to the same amount of PAR virtually applied at constant intensity over the day, the actual light climate was less effective than the theoretical which was calculated from the light response curves of assimilation (Table 6).

Whereas about 80 and 70% of the theoretical carbon net uptake was actually achieved under the canopies of the natural forest and the *Pinus* plantation at sunny conditions, only 53% were measured under that of *Eucalyptus*. Under cloudy conditions, when the proportion of diffuse light is higher and therefore light conditions are getting more favourable, the corresponding values were 86, 97 and 72% for the natural forest, the *Pinus* plantation and the *Eucalyptus* plantation, respectively.

4.2.6 Effect of sunflecks and diffuse PAR on carbon uptake

For a detailed assessment of the physiological significance of the radiation intensity and distribution below the canopies of the three forest types, 59 daily courses of PAR intensity were analyzed, which had been measured together with net CO_2 uptake (Table 7). Daily sub-canopy PAR sums less than 1 mol m^{-2} d^{-1} have been reported for dense neotropical forests (Chazdon and Fetcher 1984; Chazdon 1986). The observed mean value of 1.5 mol m^{-2} d^{-1} indicated a closed though relatively thin canopy of the natural Munessa-Shashamene Forest. The light climate to which the *Podocarpus* saplings were subjected in the *Eucalyptus* plantation was less favourable, exceeding 1.0 mol PAR m^{-2} d^{-1} only slightly and only on sunny days. Nearly twice as much PAR was recorded under the *Pinus* canopy, but CO_2 net uptake of the saplings increased only by one third, compared to the *Eucalyptus* site. With respect to photosynthetic carbon gain, not only the accumulated daily amounts of PAR are important but also the shares of diffuse radiation and sunflecks of the daily light supply (Chazdon 1986; Chazdon and Pearcy 1986b; Pearcy and Pfitsch 1994; Kueppers et al. 1996). Diffuse radiation is supposed to be related to the more equable distribution of light in the canopy (Alton 2008; Knohl and Baldocchi 2008), and in contrast to the majority of sunflecks, it is usually in the range of the linear response of photosynthesis to light intensity and thus of high photosynthetic

quantum efficiency. Sunflecks were counted as individual events when PAR intensities exceeded 40 µmol m^{-2} s^{-1} (Chazdon and Fetcher 1984; Weber et al. 1985; Chazdon 1986; Pfitsch and Pearcy 1992; Valladares et al. 1997). Although the average number of sunflecks were in a similar range of 30 to 40 per day in all three forest types and not necessarily higher on sunny than on cloudy days, the average daily sums of PAR are consistently higher on sunny days. Due to differences in the structure and density of the canopies, the duration and intensities of sunflecks and thus their contributions to the daily accumulated PAR were different. In long lightflecks, more carbon is fixed through the light phase, but at a lower quantum use efficiency (Pearcy 1988; Kueppers and Schneider 1993), whereas in a lightfleck with short duration, most of the carbon was assimilated after the lightfleck (Kueppers et al. 1996). Long-lasting sunflecks of high intensity were recorded under the *Pinus* canopy (see Figure 28 c) and to some extent also in the natural forest (Figure 28 a). There, the contributions of long-lasting sunflecks to the total daily PAR sums were rather high (55 - 72%), whereas under the *Eucalyptus* canopy the share of the sunflecks, which were shorter and less intense than in the other sites, was significantly smaller (40 - 51%) (Table 7). Even the contribution of highly effective sunflecks within the linear part of the light response curve (70 - 100 µmol m^{-2} s^{-1}) was low (6%) under the *Eucalyptus* canopy, as the proportion of sunflecks in the curvilinear part up to light saturation was about 21%, and sunflecks above light saturation of CO_2 uptake were hardly found (Figure 27). Conversely, the contribution of the diffuse radiation to the light climate under the *Eucalyptus* canopy was significantly higher, whereas in the *Pinus* plantation less than 30% were from diffuse radiation. Under *Pinus* the most effective sunflecks had the highest share, compared to the other two sites. Also a high proportion (8%) of sunflecks exceeding light saturation which decrease photosynthetic quantum yield were recorded under the *Pinus* canopy, but the time-share of these sunflecks in the daily light period was low (2%). In the natural forest, nearly as many sunflecks as in the *Pinus* site occurred, but the associated time period was shorter.

The differences in the photosynthetic efficiencies of the three sub-canopy light climates become understandable on the background of the experiment with the artificial lightflecks. Only around 30% of the daily carbon uptake by the *Podocarpus* saplings in the *Eucalyptus* plantation resulted from sunflecks and 70% from the more effective low-energy diffuse radiation, whereas considerably higher shares of sunfleck-driven and with regard to yield less effective photosynthesis were recorded in the natural forest and particular in the *Pinus* plantation.

4.2.7 Water relations - supply and consumption

The *Pinus* plantation appeared as the driest of the three forests (Table 3), but the differences in VPD and temperature to the other 2 forest types were only small. As mentioned before, the slightly higher ^{13}C values of the *Podocarpus* leaves from the *Pinus* plantation (Table 10) might indicate a somewhat higher effect of stomatal closure on the photosynthetic carbon gain than in the natural and the *Eucalyptus* forest. The respective *Pinus patula* shelter-trees did not show such indications of temporarily water shortage, as their needles had the lowest ^{13}C values of all examined leaf samples. Such differences in the overall water relations could be due to an unlimited water supply to the shelter-trees, e.g. from deeper soil horizons which were not accessible to the roots of the young *Podocarpus* trees. However, it could also result from different capacities of *Podocarpus* and *Pinus* to store water in the stems and axial tissues. The daily courses of transpiration and sap flow (Figure 41 and Figure 42) show that both species store water in their stem tissues, since in both species the onset of transpiration precedes sap flow. However, the relative amount of water which can be stored in the axial tissue cannot be concluded from these curves. In that case “relative amount” means both relative to the volume of the axial tissue and relative to the transpiring foliage. From the rates of sap flow measured after termination of transpiration both tree species may store a considerable reserve of water in their stems.

Here, for the first time, data on the total water consumption of young *Podocarpus falcatus* trees are presented and compared with that of medium-sized *Podocarpus* trees, as well as with adult *Pinus patula* and uncoppiced and coppiced *Eucalyptus saligna* shelter-trees (Table 9). Due to the irregular stem cross-section of adult *Podocarpus* trees with many vertical strands each with a diameter of several decimetres, the water demand of such a 40 – 50 m high giant individual cannot be measured. The data of the saplings as well as of the medium-size trees (which still had a round cross-section and therefore could be investigated) indicate that the daily water consumption of *Podocarpus* is high and - as far as the data allow a comparison – up to two times as that of *Eucalyptus* trees of similar diameter. As an estimate, an about 5 to 7 m high young *Podocarpus* tree at Kuke consumes 6 – 7 l on a rainy day and about 10 l on a sunny day, while a 37 years old and 35 m high *Pinus patula* consumes 20 and 33 l, respectively. A similarly big *Eucalyptus* tree transpires about 21 l on a rainy and 28 l on a sunny day. Those values are comparable with the amounts of daily water consumption of *Pinus* and *Eucalyptus* trees of other studies (Ford et al. 2004; Verbeeck et al. 2007). It should be mentioned that stem flux of *Pinus* and *Eucalyptus* were determined using the

equation and the calibration coefficient K developed by Granier (Granier 1985; Granier et al. 1996). However, for *Podocarpus*, no coefficient K was known. Therefore K was determined experimentally, following the procedure of Bush (Bush et al. 2010). With a value for K as published by Granier (Granier 1985) for Gymnosperms, sap flow density of *Podocarpus* would be underestimated about 50%.

These data do not corroborate the widely accepted idea that *Eucalyptus* plantations due to the high water demand may be detrimental for the ecosystem (Poore 1985; Florence 1986; Little et al. 2009). Other authors (Haggar et al. 1997; Parrotta 1997; Montagnini 2001; Healey and Gara 2003; Yirdaw and Luukkanen 2003; Cusack and Montagnini 2004; Lemenih et al. 2004; Lemenih and Teketay 2005) have shown that the effects of *Eucalyptus* on the environment depend on several factors, one of which is the effect on the quality of the soil rather than a high water consumption.

Once the water reserves deposited in the stem (and branches) have been transpired, sap flow commences. It is a measure of whole-tree transpiration, and reacts with a delay of less than 1 hour to the changes in VPD, as long as redelivery of water from the roots is sufficient (Figure 41 A). These conclusions explain the daily courses of sap flow, as shown in Figure 31 to Figure 33. On a first glance the midday depression found with the *Podocarpus* saplings and with *Pinus* and *Eucalyptus* on a rainy day and the lack of such depression on sunny days (all species and individuals) seems to contradict the textbook knowledge. However, kinetics of the sap flow on the rainy days coincide (with the above mentioned delay) closely with the changes in VPD in all cases were this variable could be measured (Figure 31 to Figure 33, Figure 41). A drop in VPD upon a rain shower or upcoming heavy clouds at noon resulted in a drop in transpiration and in turn also of sap flow. On the other hand, on sunny days transpiration coincides with stomatal conductance and partly with VPD, but the correlation with sap flow is less clear (Figure 41 B). As shown by Figure 31 to Figure 33, VPD increased on sunny days until late in the afternoon, while sap flow decreased continuously from noon on. This kinetics suggests a limitation of sap flow by an insufficient supply of water from the roots, resulting in stomatal closure. Although VPD has not been determined in the crown of the shelter-trees, sap flow showed in principle the same kinetics as the *Podocarpus* saplings. In detail these relations are obvious in the example shown in Figure 41 B when stomatal aperture and transpiration drastically decreased, as well as - with a delay - also sap flow, while VPD remained high.

Finally, considering water relations and the shelter-tree effect, the question arises whether there is competition for soil water between the *Podocarpus* saplings and the shelter-trees whose daily water consume is considerably higher (Table 9). While during

the rainy season the matric water potential of the soil is between 0 and -15 kPa, it decreases down to -60 kPa at the end of the dry season (Fritzsche et al. 2006). Expectedly there is a delay by up to 3 months of the seasonal changes in matric potential at depths deeper than 1 m, but the potentials as such appear more or less independent of the soil depth (down to 2 m) (Mohan et al. 1993) and the range of the seasonal changes are comparatively small. Unfortunately the horizontal and vertical extensions of the root systems, in particular of the living fine roots, are not sufficiently known. Data from the Kuke site are available for *Podocarpus* and *Eucalyptus* (Fritzsche et al. 2006), but not for *Pinus patula*. In general, representatives of the genus *Pinus* are known as tap root plants (Coutts et al. 1998), but the highest fine roots densities are always found in the upper soil horizons, mostly in the litter layer (Dames et al. 2002). This may be due to the higher nutrient content of the litter layer which is exploited by the ectotrophic mycorrhiza. However, compared to other tropical trees, fine-root biomass of *Pinus patula* in the upper soil layer is small (Valverde-Barrantes et al. 2009). Irrespective of that, *Pinus patula* is capable of water uptake from both the upper organic soil layers and from very deep mineral soil horizons. *Podocarpus falcatus* is also a taproot plant, however with tap roots rarely extending deeper than 1.5 – 2 m. High densities of fine roots have been determined along the entire taproot (Fritzsche et al. 2006), but especially so in the upper 10 cm where peaks of fine root growth have been recorded particularly during the dry season. The root system of *Eucalyptus saligna* is mainly shallow (Rob 2004), extending horizontally from the bole while only a few strong roots anchor the tree deeper in the soil. According to preliminary $\delta^{18}O$ isotope studies during the dry season in 2002 *Eucalyptus* took up soil water preferentially from soil layers below 20 cm while *Podocarpus* appeared to tap the topsoil (Fritzsche et al. 2006). Unfortunately these studies have not yet been repeated. Considering the generally small matric potential of less than -1 bar of the soil layers harbouring the major parts of the root systems and the different distributions of the fine roots in the soil, competition for soil water between the *Podocarpus* saplings and the shelter-tree species may not be very pronounced. Nevertheless it should be mentioned that sap flow in the saplings (and the smallest of the *Podocarpus* shelter-trees as well) and stomatal conductance started earlier to decrease in the course of the day than that in the shelter-trees. A significant difference between the situations in the three forests was not visible.

4.3 Conclusion

The so called “nurse-tree effect” of two exotic species and of the indigenous trees in the natural forest on the growth of *Podocarpus falcatus* saplings could be traced down to a conversion of the high global radiation into a beneficial light climate while other variables of the climate were less affected. The presented results do not support the opinion of a detrimental effect of *Pinus* on the establishment and growth of *Podocarpus falcatus*. However, such conclusions could be drawn from the performance of *Podocarpus falcatus* under the shelter of *Eucalyptus saligna*. In that case, the two-tiered canopy of the shelter-trees absorbed significantly more PAR than the other two canopies and thus per se gave rise to a lower photosynthetic production. However, not only photosynthesis was reduced under the shelter of *Eucalyptus,* but also growth, compared to the *Pinus* plantation. In contrast to the situation in the *Pinus* site, where the trees are usually felled after 30 to 40 years of growth, the *Eucalyptus* trees are regularly coppiced in 7 years intervals. When this happens the *Podocarpus* saplings shoot up (Feyera et al. 2002), making use of the improved radiation. Although data are not yet available, the jerky growth modus of *Podocarpus* saplings in the *Eucalyptus* plantation may be, on the whole, not less effective than the more even growth under *Pinus* or in the natural forest.

Nurse-trees are usually seen to provide nutrients through litter and sediment accumulation, higher mineralization rate, nitrogen transfer and increase formation of ectomycorrhiza (Padilla and Pugnaire 2006) or provide water through hydraulic lift (Prieto et al. in press). In related studies in the Munessa-Shashamene Forest sharing of mycorrhiza between *Podocarpus* and the exotic tree species could be excluded (Wubet et al. 2009), as well as a better nutrient supply from the soils in the plantation (Fritzsche et al. 2006; Freier et al. 2010). In the case of our study, it turned out that the positive effect of the plantation trees was due to the more beneficial light climate, caused by the canopies of the trees. From a scientific viewpoint to use the term “shelter-tree effect” would be more appropriate than “nurse-tree effect”.

5 Summary

Ethiopian forests disappear with a rate of 1.1% per year due to the high demand of firewood and timber. To protect the remaining parts of the forests and to meet the requirements of the population, fast growing exotic tree plantations were established 60 years ago. But there are considerable concerns regarding exotic plantations: they are vulnerable to pest calamities and have the reputation to cause damage to the ecosystems due to high demand of water and nutrients, and the release of allelopathic substances. Considering the environmental deterioration caused by monotonous plantations of exotic tree species, the chance for indigenous woody plants to rejuvenate naturally in those plantations appears to be very small. But there are observations of indigenous tree species regenerating under the shelter of exotic tree plantation of pine and eucalypts. This enhanced growth of indigenous saplings under the canopy of exotics has been termed “nurse-tree effect”.

In the Munessa-Shashamene Forest, a tropical montane forest in Ethiopia consisting of plantations of exotic tree species and remnants of disturbed natural forest, regeneration and an enhanced growth of native *Podocarpus falcatus* saplings under the shelter of exotic tree plantations (*Pinus* and *Eucalyptus*) was observed. The focus of this work was to examine the different growth patterns of the saplings in the sites, the effects of the microclimate (radiation, temperature, relative humidity, vapour pressure deficit (VPD) and throughfall) on the photosynthetic performance, and to compare the water relations of the *Podocarpus* saplings and those of the shelter-trees. Plots were established in the two plantations and in the natural forest to investigate the nurse-tree situation in the three sites, of which the natural forest was considered as a control. At the beginning of the study the *Podocarpus falcatus* saplings in the three sites had a diameter at breast height (dbh) between 1.0 and 8.7 cm and a height between 0.8 and 9.7 m. The results of the study are summarized as follows:

1. Observations over two years showed that the relative growth rates of the saplings were more than three times higher in the *Pinus* plantation, whereas in the natural forest and the *Eucalyptus* site relative growth rates were statistically not different. Thus, at least for the *Pinus* plantation, a significant shelter-tree effect could be verified[3]. Relative growth rates during the dry and the rainy season were more or less identical.

[3] For comment on the „nurse-tree effect“ of *Eucalyptus* see 8.

2. Investigation of the sub-canopy microclimate proved PAR and VPD as major components with impact on the photosynthetic performance of the saplings. 71% of the variations in photosynthetic carbon uptake could be explained by PAR and 4% by VPD.

   Air temperature and relative humidity did not differ greatly between the forest types. The *Pinus* plantation was slightly warmer and drier compared to the other two sites, which is also indicated by the slightly higher $\delta\ ^{13}C$ ratio of the *Podocarpus* leaves from the saplings in the *Pinus* plantation. Due to the varying densities of the canopies reaching 99% in the natural forest, 68 and 72 % in the *Pinus* and *Eucalyptus* plantations[4], respectively, irradiance under the canopies was different.
3. Sub-canopy radiation is composed of diffuse light and of direct radiation by sunflecks. For an assessment of the photosynthetic efficiency of the light climate, light response curves of photosynthetic net CO_2 uptake were produced and the efficacy of the individual shares of the irradiation were determined from these curves. The time spans and distribution of these shares of the daily accumulated radiation were recorded from the daily courses. The photosynthetic efficacy of the diffuse radiation was compared with that of the sunflecks. It turned out that photosynthetic active radiation (PAR), provided only as diffuse radiation of low intensity, would increase the photosynthetic carbon gain by about 30%. Lower quantum efficiency of the sunflecks resulted from their high intensity which exceeded the linear section of the light response curve. Daily accumulated CO_2 uptake was compared with a theoretical optimum under the individual canopies to determine the respective quantum efficiencies. Generally, quantum efficiencies were higher under rainy season conditions when the intensities of the sunflecks were lower.
4. Highest PAR values of all sites were recorded in the *Pinus* plantation. However the efficiency of the radiation was relatively low (70%), because of the high intensity of the sunflecks, especially during the dry season. On cloudy days (which dominated during the very moist year 2006), the efficiency was nearly 100% and resulted in an optimum photosynthetic performance of the saplings in the *Pinus* plantation. In both seasons, the percentage of daily accumulated PAR resulting from sunflecks was high (72%).

[4] The investigated *Eucalyptus* plot had partially a two-tired canopy from the original trees and the trees which had regrown after coppicing.

In the *Eucalyptus* plantation, PAR values were the lowest of the three sites. The two-tired canopy of coppiced and uncoppiced *Eucalyptus* trees resulted in a higher proportion of diffuse radiation and less daily accumulated PAR from sunflecks (46%). Also the efficiency of the actual radiation was the lowest of all sites on cloudy (72%) and sunny (53%) days.

Daily accumulated PAR under the canopy of the natural forest was in between the other forest types. Such mid-position was also true for the share of the sunflecks and the CO_2 uptake. Efficacy of the radiation was 80% on sunny and 86% on cloudy days. The total carbon gain by the *Podocarpus* saplings was about the same on dry season and wet season days.

5. Water relations can substantially affect the photosynthetic performance of plants. Especially in the afternoons of the dry season a decrease of photosynthetic CO_2 uptake by the *Podocarpus* saplings became apparent. Whole-tree water consumption was determined by measuring sap flow with the Granier system. To that end the system had to be calibrated for *Podocarpus.* In principle sap flow (and transpiration) followed VPD. However, due to water stored in the axial tissue of *Podocarpus* and *Pinus* sap flow was temporally shifted, beginning later in the morning than transpiration and lasting longer in the evening. A 5 - 7 m high *Podocarpus* sapling consumed 6 - 7 l water on a rainy and up to 14 l on a sunny day, whereas a 17 m high *Podocarpus* shelter-tree transpired 8 to 22 l per day, depending on the season. The corresponding amounts of water consumption were 20 and 35 l, respectively, for a 35 m high *Pinus patula*, and 21 and 28 l for a comparable *Eucalyptus* tree.
6. Comparison of the daily courses of transpiration and stomatal conductance and sap flow showed an earlier decrease of transpiration by the leaves of the saplings than by the shelter-trees, suggesting slight water shortage especially during the dry season. This interpretation is corroborated by the higher ^{13}C values in the leaf tissue of the saplings from the *Pinus* plantation. Nevertheless severe drought stress did not occur during the two years of investigation and competition between the *Podocarpus* saplings and the shelter-trees for soil water appears to play a minor role.
7. The literature on the „nurse-tree effect“ mentions in particular *Eucalyptus* as shelter-tree, a finding which is not in agreement with the data of this study: Neither photosynthesis nor growth was enhanced compared with the control saplings in the natural forest. The discrepancy between this work and the literature can be solved when the management of the *Eucalyptus* plantation is

considered. As long as the *Podocarpus* saplings grow under the two-tired canopy of the coppiced trees, growth is as slow as in the natural forest. However, after coppicing the light climate for the saplings ameliorates considerably and growth rates increase. Although the investigated *Eucalyptus* plantation was not coppiced during the time of the present study, the positive effect on the growth of the *Podocarpus* saplings could be observed in another part of the Munessa-Shashamene Forest. Thus, a shelter-tree effect could also be observed under *Eucalyptus*, but its dynamics is stepwise rather than continuous.

8. The shelter-tree effect of *Pinus patula* and *Eucalyptus saligna* (and presumably also other species) in *Podocarpus falcatus* could be used for an improved forest management introducing a rotation between the exotic shelter-trees and the indigenous *Podocarpus*. Faster recruitment and growth of *Podocarpus* under the shelter would provide an already established young *Podocarpus* forest upon clear-felling of the exotic trees. Such rotation, in addition to the production of *Podocarpus* as a plantation tree, would also counteract the alienation of the original ecosystem.

6 Zusammenfassung

Die Restbestände der Naturwälder Äthiopiens schrumpfen durch die mit dem Bevölkerungswachstum steigende Nachfrage nach Feuer- und Bauholz mit einer Rate von 1,1 % pro Jahr. Um die verbleibenden Wälder zu schützen und zugleich den Ansprüchen der Bevölkerung gerecht zu werden, wurden vor 60 Jahren Plantagen mit schnell wachsenden exotischen Baumarten wie Zypresse, Kiefer oder Eukalyptus angelegt. Allerdings gibt es besonders in den Tropen schwerwiegende ökologische Bedenken gegen Monokulturen exotischer Baumarten: sie sind anfällig gegen Schädlingsbefall und derartige Kalamitäten sind in den (tropischen) Entwicklungsländern besonders schwerwiegend. Außerdem stehen besonders die exotischen Eukalyptusplantagen in dem Ruf, Ökosysteme aufgrund des hohen Wasser- und Nährstoffverbrauchs einseitig zu belasten und durch die Abgabe allelopathischer Substanzen das Aufkommen natürlicher Vegetation zu verhindern. Dies gilt insbesondere für indigene Baumarten, die an die Bedingungen in den natürlichen Ökosystemen angepasst sind. Dennoch gibt es Berichte, dass einheimische Baumarten unter dem Kronendach von Monokulturen exotischer Baumarten Fuß fassen können und dann sogar schneller heranwachsen als im Naturwald. Dieses unerwartete Phänomen ist in die Literatur als „Nurse-tree effect“ (Ammenbaum- oder Kronendacheffekt) eingegangen.

Im Munessa-Shashamene Wald, einem tropischen Bergwald im zentralen Äthiopien, wird ein Drittel des ursprünglichen Waldgebiets mittlerweile von Plantagen eingenommen. Der verbliebene Naturwald ist durch menschliche Nutzung an verschiedenen Stellen stark gestört. In Höhenlagen um 2000 m dominiert im Naturwald die Steineibe (*Podocarpus falcatus*). Aufgeforstet wird ausschließlich mit exotischen schnellwüchsigen Baumarten: *Cupressus lusitanica*, *Pinus patula* und *Eucalyptus saligna.* Während der sehr dicht gepflanzte Zypressenforst kaum Unterwuchs hat, zeigt sich im Kiefern- und Eukalyptusforst beträchtliche Naturverjüngung von *Podocarpus*. Ziel der vorliegenden Arbeit war es, das unterschiedliche Wachstumsverhalten des *Podocarpus*-Jungwuchses unter den Kronendächern einer Kiefer- und einer Eukalyptusplantage zu erfassen und mit dem Wachstum von Jungbäumen im Naturwald zu vergleichen. Des weiteren sollte zur Verifizierung des Kronendacheffekts für diesen eine ökophysiologische Erklärung gefunden werden. Zu diesem Zweck wurde der Effekt des jeweiligen Mikroklimas (Strahlung, Temperatur, relative Luftfeuchte, Wasserdampf-

Sättigungsdefizit der Luft und Bestandesniederschlag) auf die Photosyntheseleistung der jungen Bäume unter den verschiedenen Kronendächern untersucht und mit der Leistung der „Ammenbäume“ verglichen. Ebenso wurde der Wasserhaushalt des *Podocarpus*-Jungwuchses und der Ammenbäume untersucht. Dafür wurden in den zwei Plantagen und im Naturwald Untersuchungsflächen mit mehreren jungen Steineiben und Kronenbäumen eingerichtet. Die Untersuchungsfläche im Naturwald diente als Kontrolle für den Kronendacheffekt. Da es sich um Naturverjüngung handelt, waren die jungen Podocarpus-Bäume unregelmäßig im Plot verteilt und auch unterschiedlich alt und groß. Zu Beginn der Studie hatte der *Podocarpus*-Jungwuchs in den drei Beständen einen Brusthöhendurchmesser zwischen 1,0 und 8,7 cm und eine Höhe zwischen 0,8 und 9,7 m. Im folgenden sind die Ergebnisse der Arbeit dargestellt:

1. Im zweijährigen Untersuchungszeitraum zeigte sich, dass die relativen Wachstumsraten der jungen Steineiben in der Kiefernplantage dreimal höher waren als die im Naturwald und in der Eukalyptusplantage. Damit war der Kronendacheffekt zumindest für die *Pinus*-Plantage[5] bestätigt. Unterschiede im Wachstum in der Regen- und Trockenzeit traten nicht auf.
2. Es wurde festgestellt, dass die für die Photosynthese wichtigsten Komponenten des Mikroklimas die Strahlung (PAR) und das Sättigungsdefizit der Luft sind, durch welche jeweils 71% und 4% der Unterschiede bei der Kohlendioxidaufnahme erklärt werden können.

   Der Vergleich des Mikroklimas an den drei Standorten zeigte, dass die Kiefernplantage im Gegensatz zu den anderen beiden Standorten etwas wärmer und trockener war. Diese Tendenz bestätigte sich auch durch die etwas höhere Isotopenverhältnis der Blätter des *Podocarpus*-Jungwuchses in der Kiefernplantage ($\delta\ ^{13}C$: -28.6‰ gegenüber -29.4‰ von *Podocarpus*-Blättern aus dem Naturwald).

   Unterschiedlich waren allerdings die Strahlungsverluste beim Lichtdurchtritt durch die 3 Kronendächer. Das zu 99% geschlossene Kronendach des Naturwaldes ließ 0,8% der Gesamtstrahlung passieren, während die Durchlässigkeit der eher lückigen Kronendächer der Pinus- und der Eukalyptusplantage mit 2,6% und 3,4% der Gesamtstrahlung höher war. Allerdings gab es in der Eukalyptusplantage ein zweites tiefer gelegenes Kronendach von denjenigen Eukalyptus-Bäumen, die nach dem „Auf-Stock-

[5] Über den Kronendacheffekt unter *Eucalyptus* s. 7.

setzen“ wieder ausgetrieben hatten. Dadurch war der Lichtgewinn bei einigen *Podocarpus* Jungbäumen noch geringer als der im Naturwald.

3. Die im Vergleich zur Gesamtstrahlung geringfügige Strahlung unter den Baumkronen setzt sich aus der diffusen Himmelsstrahlung und der direkten Strahlung in den das Kronendach durchdringenden Lichtstrahlen, den sog. Lichtflecken, zusammen. Zur Beurteilung der photosynthetischen Wirksamkeit des Lichtklimas wurden Lichtsättigungskurven der Netto-CO_2-Aufnahme bei gleichbleibenden äußeren Bedingungen aufgenommen und die Wirksamkeit der diffusen Strahlung und der Lichtflecken anhand der Lichtsättigungskurven berechnet. Dazu wurden die Strahlungsmengen in Anteile bestimmter Intensitäten zerlegt, deren Bereiche sich aus den Sättigungskurven ergaben. Die Dauer und Verteilung über den Tag dieser Strahlungspakete wurden aus gemessenen Tagesgängen der Lichtintensitäten ermittelt. In einem Simulationsexperiment wurde die photosynthetische Wirksamkeit von Lichtflecken mit derjenigen der diffusen Strahlung verglichen. Würde man die in einem Tag akkumulierte PAR-Menge nur als gleichbleibende diffuse Strahlung anbieten, so würde sich der tägliche Photosynthesegewinn um ca. 30% erhöhen, sofern keine Limitation durch die Stomata eintritt. Die geringere Quantenwirksamkeit der Lichtflecken lässt sich dadurch erklären, dass ihre Strahlungsintensitäten größenteils oberhalb des linearen Teils der Lichtsättigungskurven liegen. Die wirksamsten Lichtflecken lagen im Bereich zwischen 70 und 100 µmol m^{-2} s^{-1}. Die Ausbeute verbesserte sich unter dem bewölkten Himmel in der Regenzeit.
4. Die sich aus den Tagesgängen ergebende Tagesleistung der Photosynthese wurde mit einer aus der Lichtverteilung errechneten optimalen Nutzung der Lichtmenge verglichen, um die tatsächliche photosynthetische Lichtausnutzung unter den verschiedenen Kronendächern zu ermitteln.

   Die höchsten Strahlungswerte (PAR) wurden in der Kiefernplantage gemessen. Wegen der hohen Intensität der Lichtflecken, vor allem in der Trockenzeit, war die photosythetische Effizienz der Strahlung allerdings verhältnismäßig gering (70%), denn der Anteil der Lichtflecken an der gesamten Strahlungssumme eines Tages war unter dem Kronendach der Kiefern sehr hoch (72%). Unter bewölktem Himmel, d.h. unter Regenzeit-Wetterbedingungen (die aufgrund der langen Regenperiode von März bis Oktober im Jahr 2006 vorherrschten), war die Effizienz jedoch fast 100%.

In der Eukalyptusplantage waren die Strahlungssummen im Vergleich zu den anderen Standorten am niedrigsten. Allerdings führte das doppelte Kronendach, dass durch das „Auf-Stock-Setzen“ der *Eukalyptus*bäume zustande kommt, zu einem höheren Anteil von diffuser Strahlung und einem niedrigeren Anteil aus Lichtflecken (46%). Ebenso war die Ausnutzung der gemessenen Strahlung mit 72% an bewölkten und 53% an sonnigen Tagen verhältnismäßig schlecht. Die täglichen Strahlungsmengen unter dem Kronendach des Naturwalds lagen zwischen denen in der Kiefern- und der Eukalyptusplantage. Die Mittelstellung galt auch für den Strahlungsanteil der Lichtflecken am Lichtklima und die CO_2-Aufnahme. Die photosynthetische Strahlungswirksamkeit lag zwischen 80 % (an Sonnentagen) und 86 % (bei Bewölkung). Anders als in den Plantagen war die Kohlenstoffaufnahme des Jungwuchses während bewölkter und sonniger Wetterbedingungen gleich.

5. Außer dem Lichtklima kann auch der Wasserhaushalt der Bäume den photosynthetischen Kohlenstoffgewinn erheblich beeinflussen. Die Tagesgänge der stomatären Leitfähigkeit der Blätter und der Transpiration wurden im Zuge der Porometermessungen mitverfolgt. Der gesamte tägliche Wasserverbrauch der Jungpflanzen und Kronenbäume wurde durch Saftflussmessungen nach der Graniermethode ermittelt. Für *Podocarpus* gibt es dazu keine Literaturdaten, weshalb eine eigene Eichung der Methode für diese Art durchgeführt wurde.

   Erwartungsgemäß war der tägliche Wasserbrauch von der Baumart, der Größe der Bäume und von den Wetterbedingungen abhängig. Im Allgemeinen korrelierte der Saftfluss mit dem Sättigungsdefizit der Luft, solange die Stomata geöffnet blieben. Dies war meist am Vormittag der Fall, während nachmittags öfters eine Verringerung der stomatären Leitfähigkeit den Wasserverbrauch (und die Photosynthese) einschränkte. Aus dem Vergleich des Tagesgangs der Transpiration und des Saftflusses kann auch auf Wasserspeicher im Stamm und Geäst der Bäume geschlossen werden. Ein solcher Speicher zeigte sich bei den *Podocarpus*- und *Pinus* Kronenbäumen, nicht aber bei *Eucalyptus*.

   Der tägliche Wasserverbrauch lag bei 5 – 7 m hohen jungen Podocarpus-Bäumen zwischen 6 – 7 l an einem regnerischen und 14 l an einem Sonnentag. Ein *Podocarpus*-Kronenbaum mit 17 m Höhe verbrauchte entsprechend 8 bzw. 22 l. Die entsprechenden Tagesmengen einer 35 m hohen *Pinus patula* lagen bei 20 bzw. 35 l und die eines vergleichbaren *Eucalyptus* bei 21 und 28 l.

6. Im Vergleich der Transpiration mit den Saftflussraten und der stomatären Leitfähigkeit zeigte sich eine Verringerung sowohl der Transpirationsraten als

auch der stomatären Leitfähigkeit der jungen *Podocarpus*-Bäume im Tagesgang früher als bei den Kronenbäumen. Dies spricht für eine geringfügige, d.h. temporäre Wasserknappheit, vor allem in der Trockenzeit. Beim *Podocarpus*-Jungwuchs zeigt sich dies auch an den $\delta^{13}C$ Werten der Blätter, in denen die ^{13}C-Werte etwas höher sind als z.B. bei den Kiefern. Wassermangel im größeren Umfang tritt aber im Munessa-Shashamene Wald offensichtlich nicht auf.

7. In der einschlägigen Literatur wird ausdrücklich auf den Kronendacheffekt von Eucalyptus *saligna*- und *globulus*-Plantagen verwiesen. Im Zuge dieser Arbeit konnte eine erhöhte Photosyntheseleistung und besseres Wachstum unter *Eucalyptus* nicht festgestellt werden. Der scheinbare Widerspruch löst sich, wenn man das unterschiedliche Management von *Eucalyptus*- und *Pinus*-Plantagen berücksichtigt. Solange der *Podocarpus* Jungwuchs unter dem zweistöckigen *Eucalyptus*-Kronendach aufwächst, ist das Wachstum nicht schneller als im Naturwald. Nach dem „Auf-Stock-Setzen“ jedoch verbessern sich die Lichtverhältnisse umgehend und die inzwischen mehrjährigen *Podocarpus* Pflanzen reagieren mit einem enormen Wachstumsschub. Leider ergab sich diese Situation nicht während der Bearbeitungszeit dieser Studie, aber entsprechende Beobachtungen wurden in anderen Gebieten des Munessa-Shashamene Waldes gemacht. Insgesamt ergibt sich also doch ein Kronendacheffekt, der allerdings aus Perioden langsamen Wachstums im Wechsel mit schnellen Wachstumsschüben resultiert.
8. Der Kronendacheffekt unter *Pinus patula und Eucalyptus saligna könnte* für ein Forstmanagement genutzt werden, in dem exotische schnellwüchsige Baumarten mit der wertvollen einheimischen Steineibe abwechseln. Durch den schnelleren Aufwuchs von *Podocarpus unter d*em Kronendach würden beim Fällen der Plantage die bereits gut etablierten Steineiben die nächste Forstgeneration darstellen. Zunächst könnte man zur Samenproduktion kleinere „natürliche Bestände“, wie sie jetzt unter dem Kronendach der Plantagen entstanden sind, nach dem Kahlschlag weiter heranwachsen lassen, um mit dem Saatgut die systematische Rotation einzuleiten.

   Mit einer solchen würde man auch der befürchteten ökologischen Verfremdung des Waldgebiets entgegen wirken.

7 Literature

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Declaration

Hiermit erkläre ich, dass ich die Arbeit selbständig verfasst und keine anderen als die von mir angegebenen Quellen und Hilfsmittel verwendet habe. Des weiteren versichere ich, dass ich weder diese noch eine andere gleichartige Doktorprüfung an einer anderen Hochschule endgültig nicht bestanden habe.

Simone Strobl

Bayreuth, den 19. März 2012